ORIENTATION BY JUMPING SPIDERS OF THE GENUS *Phidippus* (ARANEAE: SALTICIDAE) DURING THE PURSUIT OF PREY

By

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Jumping spiders of the genus *Phidippus* tend to occupy waiting positions on plants. From these reconnaissance positions, the spiders are often required to utilize indirect routes of access (detours) to attain a position from which sighted prey (*primary objective*) can be captured.

Selection of an appropriate route of access is based upon movement toward a visually determined *secondary objective* (plant configuration), which may provide access to the prey position. In moving toward a secondary objective, the spider must turn away from the prey. At all times during a pursuit, the spider retains a memory of the relative position of the prey in space, with respect to several spider-centered reference systems which are available for the determination of direction. This memory of prey position is frequently expressed in the form of a *reorientation turn* directed toward the expected position of the prey. Each reorientation turn initiates a new *segment* of the pursuit.

Phidippus can employ the immediate direction (route) of pursuit, the force of gravity, and a radial direction with respect to the route perceived through visual cues (including those cues furnished by both the background and the immediate plant configuration) as reference directions, for memory of the relative position of the prey. *Phidippus* also compensate for their own movement in these reference systems in determining a reorientation direction.

The indirect pursuit of sighted positions is a general feature of the movement of *Phidippus* in vegetation, and the same reference systems for reorientation that are employed during the pursuit of prey can assuredly be applied to visually directed movement in general.

SECTION I
INTRODUCTION

Salticid spiders utilize their highly developed vision to locate, evaluate, and pursue potential prey. Since most of these spiders dwell on plants, where the approach to prey is seldom in the form of a straight line, effective access to prey requires an ability to utilize an indirect route of pursuit.

Heil (1936) was the first to appreciate the significance of such detoured routes, in his studies of the salticids *Evarcha marcgravi* and *E. blancardi* [currently *E. arcuata* (Clerck) and *E. falcata* (Clerck), respectively]. Heil's insight into the remarkable ability of salticids to locate and utilize a detour during the pursuit of prey probably owed as much to his extensive observations of *Evarcha* in the field as it did to his documentation of detour behavior in the laboratory. Unfortunately, his observations of what he termed one of the higher accomplishments of the salticids have received no attention in the subsequent literature. Apart from a singular account of the circuitous approach of a *Phidippus audax* in pursuit of a grasshopper (Bilsing, 1920), there is essentially no additional literature on the subject.

A salticid requires an accurate memory for the relative position of prey in space if it is to utilize a detour of any complexity beyond that involved in a simple approach where prey is subject to visual survey at all times. The objectives of this study include the evaluation of the ability of certain salticid spiders (*Phidippus*) to determine and successfully negotiate detours during the pursuit of prey, and the assessment of the forms of sensory information which contribute to the orientation of these spiders during such a detour.

SECTION II
MATERIALS AND METHODS

The species of Phidippus which have been observed during the course of this study are listed in Table 1. All experiments were performed with individuals of P. pulcherrimus, and many of these were repeated with other species of Phidippus to extend the generality of the results. Selection of P. pulcherrimus as the primary subject of study was based upon the ease with which these spiders adapted to laboratory situations, as well as their willingness to run pursuits under artificial conditions. This is without doubt related to the habitat of these spiders, which generally dwell upon herbacious plants in an open field. By contrast, individual P. pulcher (Walckenaer) appeared to be preoccupied with the problem of ascent and often refused to pursue prey in laboratory situations. P. pulcher are generally found living in trees.

Initially several sequences of pursuit behavior were recorded during field observation of P. princeps. Subsequently, experimental problems of prey pursuit have been utilized to increase the volume of data available for statistical evaluation.

The basic technique employed in the laboratory in the study of pursuit behavior and orientation is quite simple. Individual spiders are placed upon structures of varying design, stimulated with a dead fly cemented to the end of a long strand of hair (standard lure), and certain aspects of the ensuing behavior are recorded in a manner which

Table 1. Species of *Phidippus* observed during the course of this study.

SPECIES	COLLECTION SITE	INDIVIDUAL SPIDER NUMBERS (SN)
P. pulcherrimus Keyserling, 1884	Immatures collected from resting sacs on the herb *Euthamia minor* at Big Prairie, Ocala National Forest, Marion County, Florida. Reared to maturity.	females: 1-6 male: 7
	Offspring of animals captured at Big Prairie.	females: 8-14 males: 15-18
P. princeps (Peckham, 1883)	Immatures observed living on *Euphorbia esula* herbs at Groveland Field, Hennepin County, Minnesota.	
	Collected at Groveland, reared to maturity.	female: 19 male: 20
P. regius C. L. Koch, 1846	Collected as immatures living on herbacious plants at Big Prairie, reared to maturity.	females: 21-24 male: 25 (SN 21 and 25 are immature)
P. clarus Keyserling, 1884	Immatures collected from sweep of grasses and herbacious plants at Big Prairie, reared to maturity.	males: 26-28
P. audax (Hentz, 1845)	Adults observed along the margin of Newnan's Lake, on grasses and herbacious plants. Alachua County, Florida.	

With each presentation of experimental results, individual spiders are referred to by the numbers given at the right, above. Thus SN 24fREG refers to spider number (SN) 24, a female *P. regius*. The first three letters of each species name are included in the abbreviated title.

varies with the design of each experiment. If necessary, spiders are lured into starting positions with the same stimulus. Many of the experiments involve a determination of the direction faced by the spider, by projection of the axis of the spider onto a visible scale. This process is greatly facilitated by the relatively large size of Phidippus jumping spiders, as well as by the presence of conspicuous and symmetrical groups of light-colored scales upon the prosoma of each spider.

Unless otherwise specified, artificial lighting was provided by either 100 w or 150 w (about 1500 to 2500 lumens) incandescent light bulbs, situated inside aluminum parabolic reflecting lamps placed 0.5 to 1.5 m above each experimental situation. Laboratory temperature was consistently held near 25°C.

As noted by Kästner (1950) in his study of Evarcha falcata, individual salticids can have distinct and consistent "personalities," or individual modes of behavior as observed in a particular context. Management of spiders for the purposes of this study has been on an individual basis, as some individuals are markedly better performers in a given experimental situation than are others. Similar variation in the behavior of individuals was noted by Tryon (1940) in his study of white rats. Hundreds of spiders have been screened in the selection of the relatively few (N= 28) individuals which receive mention in this study. This selection was based solely upon whether or not the spiders would actively, and repeatedly, pursue a standard lure in laboratory situations. Virtually all Phidippus observed in the course of this study (including rejects) demonstrated an ability to run a detoured pursuit, nonetheless.

After individual screening, some attention is devoted to the care of "runners," to maintain their responsiveness at a healthy optimum. A certain degree of food deprivation is required for this purpose, but this cannot be carried to the extreme of starvation. The spiders are kept, as adults, individually in Petri dishes. They are provided with droplets of drinking water several times a week. The spiders which are being used for an experiment are provided with flies (either *Musca domestica* or vestigial-winged *Drosophila melanogaster*) and they are fed only when the opisthosoma is markedly reduced in size and starvation appears to be imminent.

Ordinary statistical methods, consistent with definitions provided by Siegel (1956), Runyon and Haber (1971), and Mendenhall and Scheaffer (1973), have been employed for the analysis of data. The chi^2 test was used for the analysis of simple enumerative data, as well as that arranged in contingency tables. For presumed parameters, means are generally presented ± 1 standard error. Student's *t* test was utilized to determine either the significance of the difference between two mean values, or the significance of the difference between one mean and a fixed value. Paired data were analyzed by means of linear least-squares regression, the Pearson *r* correlation coefficient, and the z_r test for the significance of *r*.

SECTION III
SALTICID VISION

As shown in Figure 1, salticids have eight eyes, six of which are relatively large, situated upon the prosoma. Apart from the posterior medial eyes (PME), for which a definite function has never been established, there are basically two types of eyes: the anterior medial, or principal eyes (AME), and the lateral eyes (ALE and PLE). The use of separate eyes for different functions allows for a combination of high resolution in a narrow field of vision provided by the AME (the retinae of which function as the foveae of the spider) with a wide (360^o) field of peripheral vision and lesser resolution provided by the lateral eyes (Homann, 1928; Land, 1969a, 1974).

The lateral eyes continuously survey a large field around the spider; these function as movement detectors, capable of directing a turn by the spider to face a moving stimulus with the AME (Petrunkevitch, 1907; Homann, 1928; Land, 1971; Eakin and Brandenburger, 1971; Dill, 1975). These eyes have a single spectral class of receptors, with a peak sensitivity at $\lambda = 536$ nm in Menemerus confusus (Yamashita and Takeda, 1976). In the PLE and part of the ALE, receptor separation limits the angular resolution to about 1.0^o of arc (Land, 1969a); stimulation (by a decrease in light intensity) of only two receptors, separated by at least 1.0^o, in succession can lead to a turn (facing) toward the second of the two stimuli (Evarcha arcuata; Duelli, 1975). The lateral eyes should have some additional, generalized functions,

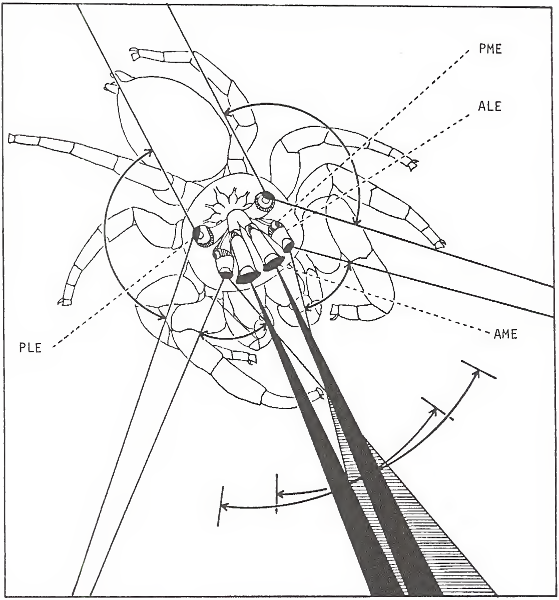


Figure 1. Diagram of the approximate visual field of Phidippus as viewed from above, showing the eyes and their respective optic nerves. This diagram is drawn from information provided by Land(1969a), Duelli (1975), and Hill (1975). The posterior lateral (PLE) and anterior lateral eyes (ALE) provide the spider with a 360° survey of the surroundings; the region of binocular overlap of the ALE in front of the spider is shaded. The diminuitive posterior medial eyes (PME) synapse primarily with a group of interneurons of large diameter (Hill, 1975), which may release a rapid escape response. The principal or anterior medial eyes (AME) possess high resolution but a restricted visual field, as shown in black. The tubular portion of each AME, including the retina, can be moved from side to side to scan the area in front of the spider as indicated by the arrows at lower right.

as each eye is connected equally to two completely different tracts of interneurons (Hill, 1975).

The remarkably large AME of salticids are demonstrably used to evaluate form in the determination of subsequent behavior, particularly in the recognition of a potential mate or potential prey (Homann, 1928; Heil, 1936; Kästner, 1950; Dzimirski, 1959). The bipolar sensory cells of each AME are situated in 4 layers at the end of a long tube; the AME bear fixed lenses but the eye tubes and retinae can be moved from side to side and rotated to either scan or center upon stationary objects, or to track moving objects (Land, 1969b). The field of vision is small (Figure 1), but the resolution of these eyes is limited only by the 0.15° angular separation of the receptors, far less than the theoretical limit (0.5°) for resolution by the compound eyes of insects (Land, 1969a, 1974). As with the lateral eyes, the depth of field of the AME in Phidippus extends from a position nearer than 5 cm to the spider to infinity (Land, 1969a).

Stratification of the retina of the salticid AME may relate to color vision (Land, 1969a). Electroretinograms and direct measurement of receptor potentials have established the presence of at least 3 distinct classes of receptors in the AME of P. regius (peak sensitivities at $\lambda = 370$ nm or UV, 532 nm or green, and 370-525 nm; DeVoe and Zvargulis, 1967; DeVoe, 1975), and at least 4 spectral classes of receptors in Menemerus confusus (peaks at $\lambda = 360$ nm or UV, 480-500 nm, 520-540 nm, and 580 nm; Yamashita and Takeda, 1976). Color recognition should, then, play a considerable role in the evaluation of conspecifics, potential prey, and even the immediate surroundings by the jumping spider. Crane (1949) and Kästner (1950) provide limited demonstrations of the role of color vision in this regard.

The problem of distance resolution or depth perception is of considerable importance with respect to the orientation of these animals; distance information is not only a critical determinant of many behaviors, such as the predatory jump, but it is also required for the accurate appraisal of the relative prey position during a pursuit run (see below).

Clearly distance resolution is a function of the front (face) eyes, the AME flanked the the ALE. Of these, the ALE have the greatest separation, as well as an overlapping field of vision (Figure 1), suggestive of binocular vision. This role is supported by the work of Homann (1928), who found that blinding of a single ALE reduced the accuracy of a jump to the same extent as the blinding of both ALE. The AME can also be demonstrated to provide a certain amount of distance information (Homann, 1928; Heil, 1936). The greater resolution of the AME is offset by the proximity of these eyes, however. Since points more than 3 cm from the spider come to focus in a single receptor layer of the AME, it is unlikely that a single AME can provide monocular (focal plane) depth perception (Land, 1972b). Presumably, in the intact spider, data from the fixed ALE and the moving AME are superimposed (integrated) and comprise a consistent view of the visual field to the front of the animal.

Compared with the wide-angle lenses of the PLE, the lenses of the ALE are of significantly longer focal length, corresponding to a more restricted field of vision to the front of the spider (Land, 1969a). Peripheral angular resolution of the ALE (determined by separation of the receptors) is comparable to that of the PLE (about 1.0° of arc), but this increases to about 0.5° for the ALE receptors which receive stimuli from the field of binocular overlap of the ALE, directly in front of the spider (Land, 1972b, 1974). Since angular resolution is critical to the resolution of distance, this feature agrees with the role of the ALE in the binocular resolution of distance.

Figure 2 provides a simple analysis of the theoretical limit to binocular resolution as a function of the separation of the eyes and the angular resolution of each eye (ALE), for a point stimulus. The length of each sampling interval increases greatly with distance (corresponding to a decrease in the accuracy of distance information), until an upper limit is reached at which no further distance can be discerned from infinity. As noted in Figure 2, one cannot set precise values for these sampling intervals, and they may vary greatly as different combinations of one receptor stimulus from each eye are compared within the central nervous system of the spider. Each combination of this sort may be termed a distance sample, which by itself can be expected to decline in accuracy as the distance from the spider increases.

An object which subtends more than a single receptor from each eye, then, can be expected to provide a series of distance samples of varying accuracy. Statistical treatment of these data within the nervous system of the spider could extend the accuracy of the distance resolution considerably. The form of a stationary housefly (*Musca domestica*) might subtend 15-20 receptors in each of the ALE at a distance of 20 cm; without any sophistication for edge information this could still provide the spider with 400 eye-to-eye combinations, or distance samples, of varying accuracy. It follows that one cannot develop a theoretical limit for the resolution of distance based

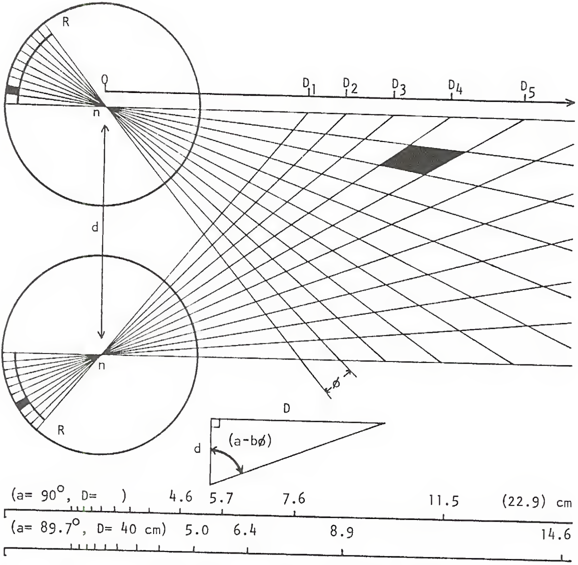


Figure 2. Resolution of distance with binocular vision. This diagram shows the retinae (R) and nodal points (n) of the ALE (large circles at left). Each of the quadrangles (sampling units) in the visual field to the right corresponds to the simultaneous stimulation of a unique pair of receptors (one from each eye) as indicated by shading. Given (ϕ), the angular resolution of the eyes, and (d), the separation of nodal points, one can determine a set of values for the limits of the distance sampling intervals (D) as indicated in the scale at the top of the diagram, by substituting integral values of (b) into the equation given above. Each value of (a) corresponds to an upper limit of (D); (a) should be chosen so that $(90^\circ - \phi) < (a) \leq (90^\circ)$. At the bottom of the figure are shown two possible scales of boundary values for distance resolution by the ALE of Phidippus, based upon $(\phi) = 0.5^\circ$ and $(d) = 0.2$ cm, with (a) and the respective upper limit of (D) indicated in each case in parentheses.

solely upon a point source of information and reasonably expect the same limit to apply to a situation where many distance samples can be made either simultaneously, or in succession. Prey moving across a visual field could provide a large amount of potential data in a short period of time. The configuration of plants near the prey position could provide an enormous amount of distance information.

Many insects can utilize parallax gained from their own movement to extend the range of their distance resolution (Horridge, 1977). There is no reason to suspect that the same does not apply to a salticid as it runs after prey. Salticids are not known to utilize distinct movements in place, such as rocking from side to side, to facilitate the resolution of distance. Phidippus generally do not move the prosoma as they survey a potential prey for an extended period of time. On occasion a spider will rotate about its axis, or tilt the prosoma during a period of sustained visual survey (Figure 3). This behavior could produce more binocular distance samples in certain situations, but the actual function of this prosomal rotation is not known.

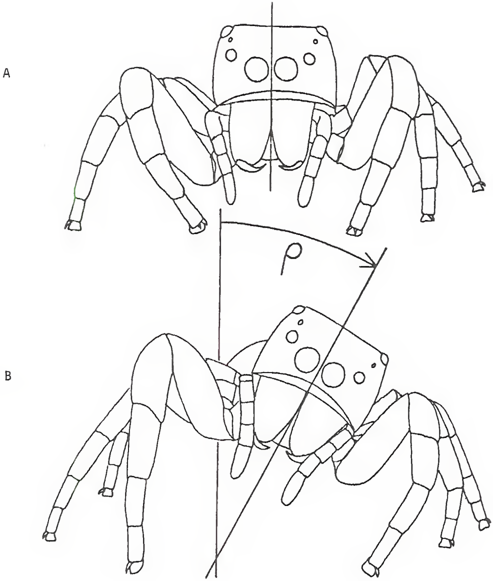


Figure 3. Phidippus before (A) and after (B) a prosomal rotation of magnitude ρ. When surveying an object, these spiders frequently tilt the prosoma to the side, as if attempting to secure some additional information. This behavior may be related to the evaluation of form by the scanning AME, but it could also be employed to improve the resolution of distance. Linear forms subtend more pairs of receptors when they are aligned with the sagittal plane of the animal, for increased distance sampling. Resolution of distance by Homo sapiens is also related to the orientation of the object relative to the axis of the head; the distance of a rod can be best determined by man when the rod is vertical with respect to a vertical sagittal plane (Blake, Camisa, and Antoinetti, 1976).

SECTION IV
THE ECONOMICS OF PREDATION: APPETITIVE BEHAVIOR

A predator may either search for prey in an active manner, or it may occupy a waiting position until the prey moves into sight, and then pursue the prey (Carthy, 1965). Although there is really a continuum of potential behavior between these two extremes, it is clear that some salticids move about actively throughout the day, while others, including Phidippus, tend to occupy waiting positions (Enders, 1975). Evarcha also assumes a waiting position in vegetation (Heil, 1936; Kästner, 1950; Plett, 1962a). At the opposite extreme is Synageles, an ant mimic, which moves about quickly with only brief intervals of pause or visual survey (Kästner, 1950). Salticus (Kästner, 1950; Drees, 1952; Plett, 1962a, 1962b) and Sitticus (Kästner, 1950) are also constant searchers.

Under certain conditions, however, it is possible for the waiting Phidippus to become an active searcher. A female P. pulcherrimus (SN 1fPUL) ran after the standard fly lure in a series of pursuits, returning after each pursuit to a waiting position, facing down in a crouch near the top of the stem. During one pursuit, this individual discovered an aphid among the terminal leaflets of a branch, and then returned to the main stem to feed. After feeding, this spider repeated the entire sequence three more times before it was interrupted, each time moving out to the terminal leaflets of various branches of the plant (Melilotus alba, or sweet clover) and conducting an extensive tactile survey marked by a constant turning and tapping of the leaflets with the forelegs, until an aphid was located and captured. It appears that Phidippus can employ this alternate (searching) strategy with some success when sedentary prey are available.

The adaptive significance of this versatility for the generalized predator of insects is evident. When the available prey are moving actively, or alighting on occasion, the spider can maximize its observation time, minimize its energy expenditure, and reduce the possibility of being captured by other predators by remaining immobile in a relatively concealed position, and pursuing prey as it appears in the area of visual survey. This is precisely the behavior that typifies many observations of Phidippus in the field. When sedentary prey are available, however, waiting is of no avail for their capture; they must be collected by a searcher.

P. princeps and P. pulcherrimus both tend to occupy waiting positions near the top of herbacious plants in an open field. These positions are generally on the main stem of the plant, facing down. The waiting position must be of fundamental importance in determining the ability of the spider to detect prey. Successful prey capture is also a function of access, or the ability of the spider to reach the prey before it escapes; access can also be related to the suitability of a waiting position.

If prey tend to appear (alight) on the upper surfaces of leaves near the top of a plant, then the spider can maximize its ability to detect prey by assuming a position near the top of the plant, facing down to survey the upper surfaces of the leaves. Regardless of where prey tended to alight, they would be most visible from above (better illumination). In addition, a spider that can jump a considerable distance *down* to its prey has a greater chance of capturing that prey if pursuit is initiated from a superior position. Thus access is also facilitated by assuming a waiting position above the area of visual survey.

If the spider waits at some distance from the main stem of a plant, it is increasing the access time required to reach every other portion of that plant by the amount of time required to reach the main stem from its waiting position. Since access time is without doubt a critical determinant of prey capture, this is a definite disadvantage. The increase in access time results from the simple fact that the main stem is the most direct avenue of approach, and in fact the only avenue of approach, which physically connects the various portions of the plant. As long as prey detection from a position on the main stem is adequate, the spider should wait on the main stem.

By the foregoing analysis one could conclude that the spider can maximize the number of prey captured per unit time by selecting a waiting position near the top of a plant stem in an open field, facing down; both prey detection and prey access should be optimal from this position. Individual *P. pulcherrimus* which have been reared for their entire lives within Petri dishes will assume and pursue prey from such a position if placed on either a vertical rod or a suitable plant. Gardner (1965) observed the use of a similar waiting position by *P. coccineus*. Greenquist and Rovner (1976) also observed a tendency for certain lycosid spiders to orient in a vertical direction, facing down, on artificial foliage. An additional feature of this position lies in the fact that the spider is facing in the direction from which other wandering spiders would necessarily approach to gain access to positions above the waiting spider; essentially (and particularly when the upper portion of the plant is isolated in an open field) the spider stands guard at the gateway to the upper portion of the plant. This may place the spider on a route utilized by potential prey, and it should at least remove the danger that another salticid is going to attack from above, since this area is presumably secure. If plants are more crowded, it could at least reduce the danger of such an attack.

Prey detection (in terms of the number of prey sighted per unit time) is also a function of the local prey density. If prey do not appear after the spider assumes a particular waiting position, then it is clearly of advantage for the spider to relocate. This response to a lack of prey is undoubtedly widespread among the sedentary spiders; as an example, Turnbull (1964) found that the theridiid Achaearanea tepidariorum will search for a new web site if prey are lacking in a given location. Plett (1962a) found that food deprivation led to greater movement by Salticus scenicus.

Likewise, individual Phidippus princeps with large opisthosomata (an index of the degree of satiation) tend to remain within or near their resting sacs (near the top of plants) throughout the day, while other individuals often move between waiting positions, far from any visible resting sacs, many times during the course of a day (Hill, 1977b). This may be viewed as a functional response to exploit regions of high prey density, since the net effect of this behavior is the concentration of the spiders in those areas where prey is most abundant.

In summary it should be noted that Phidippus, like the other salticids, is a diurnal hunter. Individuals of species which inhabit the herbacious plants of an open field tend to emerge from their resting sacs in the morning of suitable days to occupy a series of waiting positions before returning to a resting sac (or constructing a new one) for the night. The reliance of these spiders upon visual survey from a waiting position for the detection of prey implies that the ability of these spiders to pursue that prey along an available route of access is of paramount importance to their success.

SECTION V
THE PREDATORY BEHAVIOR OF SALTICID SPIDERS

If an insect appears on a flat surface, near a salticid spider waiting on that same surface, the spider will quickly turn to face the insect with the AME. If an attack follows in this situation, the spider will advance directly toward the prey at a variable but steady pace, eventually slowing to a stalk or leg by leg advance in a partially crouched position (legs drawn near to the body, thereby reducing the apparent size of the spider as viewed by the prey), with the pedipalps flickering up and down in unison. When a certain distance from the prey is attained, the spider crouches and prepares to jump by forming an attachment disk. In the case of *Phidippus*, the spider then raises legs I and II toward the prey, spreads legs III forward for balance and support during thrust, and then bends the jumping legs IV against the substratum in preparation for the moment of attack. A sudden extension of legs IV hurtles the spider into the air, toward the prey, which is impaled between the fangs and grasped with legs I and II.

Most of the descriptions of this simple attack sequence which are available in the literature are based upon the observation of captive salticids upon flat surfaces (Homann, 1928; Drees, 1952; Gardner, 1964, 1965; Hollis and Branson, 1964; Forster, 1977). Although the flat surface may be relevant to the topography encountered by a *Salticus scenicus* living on a wall during the pursuit of prey, it is not representative of the plant configurations used for access to prey by plant-dwelling Phidippus. Certain misconceptions, and particularly the incorrect notion that salticids require continuous visual (AME) contact with the prey during pursuit, can arise when one attempts to generalize from observations of attack behavior conducted exclusively upon flat surfaces. The direct pursuit which is described in this situation is obviously the best solution to the problem of access, since direct access is possible. Even in this situation, however, Phidippus may side-step around the prey to attack crawling prey just behind the moving front end. The usual, direct approach to relatively immobile prey (such as a fly which has alighted) is shown in Figure 4 (A, D); Also figured are typical sequences of pursuit which can be readily demonstrated with simple modifications of the relative positions of prey and routes of access to the position of a spider upon a flat surface.

Although the problems of pursuit which are shown in Figure 4 are rather simple, the basic features of pursuit which appear as a result have not been described previously. When a direct approach to the sighted prey (the primary objective) is not possible, the spider can alternately pursue a visible route of access (secondary objective) which is related in some way to the prey position. During this indirect pursuit, or detour, the spider retains a memory of the relative position of the prey in space; the spider can integrate information gathered during the initial observation of the prey with information pertaining to the direction and extent of its own movement (movement compensation) to determine the direction of the prey from a new position. This determination is frequently expressed in the form of a

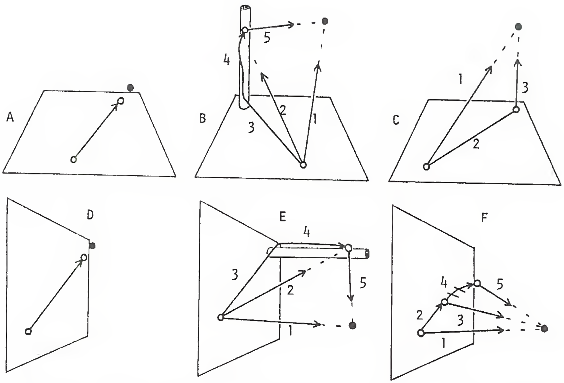


Figure 4. Behavior of *Phidippus* during prey pursuit upon flat horizontal (A-C) and vertical (D-F) surfaces. Even in relatively simple situations, one may discern the basic features of pursuit which are relevant to more complicated plant configurations. Each open circle represents a spider position; the black spots represent the position of prey, which consists of the standard dead fly dangling upon a long hair. A, D: These simple demonstrations illustrate the direct approach of the spider (vector of movement) toward prey resting upon the same surface, or near the surface; this direct approach is generally depicted as the typical or stereotyped response of a salticid to prey. B, E: With the addition of a wooden rod projecting from the surface, and the appearance of prey well away from that surface, the basic features of indirect pursuit can be observed. These include the initial turn toward the prey (1) to establish a *primary objective*, subsequent orientation toward a *secondary objective* (2) which comprises part of the route of access, a rapid pursuit oriented (visually) directly toward the base of the secondary objective (3; the base of the secondary objective could be considered to be a tertiary objective, en route to attainment of the secondary objective, en route to attainment of the primary objective, the prey), followed by ascent (4) to the secondary position and *reorientation* (5) to the primary objective. C: On a horizontal surface, the spider turns to the prey (1), turns away to run as direct a pursuit as is possible in this situation (2), and then reorients (3) to the prey. F: Behavior on a vertical surface is markedly different from that on a horizontal surface. After a turn to prey (1), the spider ascends, relative to the prey (2), reorients (3), side-steps (4), and then prepares to jump from *above* the prey (5).

reorientation turn toward the expected direction of the prey when the spider has attained a new position. Evidence for this interpretation of the indirect pursuit behavior of Phidippus will be presented in subsequent sections, along with an analysis of the types of information which can comprise a memory of the relative position of the prey by the spider, during its pursuit of that prey.

At times a spider will approach prey indirectly while maintaining visual (AME) contact with the prey, either by walking sideways (side-stepping), or by walking in a manner intermediate between forward and lateral walking. This behavior is most often observed when the spider is close to its prey. To utilize a more rapid forward run during an indirect pursuit, the spider is required to turn away from the prey, since both legs and eyes are situated on the same body unit, the prosoma. In addition, visual orientation to the indirect route of access itself, which is most evident when a jump is required along that route, precludes the use of the AME to continuously monitor the prey position during pursuit.

Implicit in this discussion is the notion that detours provide the only access to most of the area subject to visual survey by a waiting Phidippus (or Evarcha; Heil, 1936). Even with a fairly direct route of access, the actual prey position may be obscured by a leaf or stem during part of the pursuit, forcing the spider to rely upon something other than continuous visual (AME) contact to maintain its memory of the prey position. Certain forms of concealed approach (see below) which are utilized by Phidippus also require that these spiders turn away from the prey during pursuit.

Representative sequences of the indirect pursuit of prey by Phidippus are described in Figures 5-10. In each of these cases, the reorientation turns are discrete events, each executed with a single smooth movement which brings the spider to face its primary objective, or at least a fairly accurate estimate of the actual position of that objective. Figure 11 shows how a spider can attain a rather distant objective by interrupting the pursuit with a series of reorientation turns. Each reorientation turn initiates a new segment of the pursuit, and a series of segments may be required in certain situations to bring the spider into a position from which the prey can be captured. Presumably these reorientation turns are used to correct and to maintain an accurate memory of the prey position during the pursuit; like the initial orientation to prey, each reorientation can be considered to affirm the relative position of the primary objective. It is expected that there is a limitation to the ability of the individual Phidippus to maintain a memory of prey position in the absence of information provided by the object (perhaps a plant configuration associated with the prey) of reorientation, particularly when a succession of detours within the context of a detoured pursuit are required. Reorientation can also provide the spider with an opportunity to assess the merit of continuing its pursuit.

Figure 12 shows the indirect pursuit of a potential mate by a male P. audax. The use of detours by Phidippus is not restricted to the problem of access to prey, but applies more generally to the movement of these spiders in vegetation. Movement of both P. princeps and Eris marginata (Hill, 1978) in the field is frequently interrupted by periods of extensive turning, ostensibly for purposes of visual survey

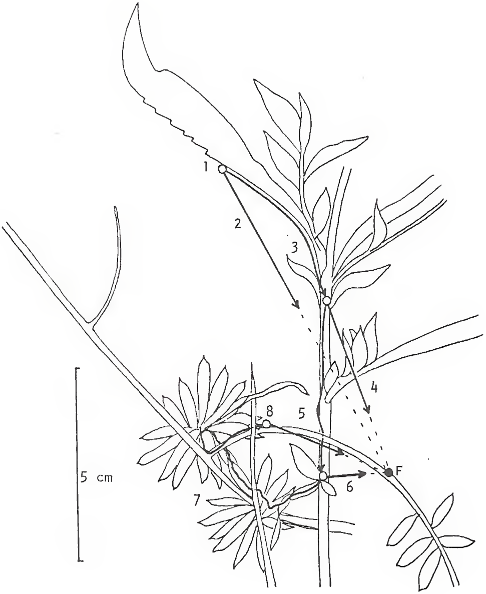


Figure 5. Indirect pursuit of prey by an immature P. princeps observed in an old field habitat, based upon field sketch and measurements of the configuration. Initially (1), the spider (open circles) rests in a waiting position beneath a Solidago leaf. Then it turns (2) to face a fly (F) which has just alighted at a distance of about 10 cm, upon a branch of Euphorbia esula. Pedipalps flicker up and down in unison as the spider surveys the fly. Subsequently the spider runs (3), reorients in a single smooth turn to the position of the immobile fly (4), runs (5), again reorients accurately (6), then climbs over a series of Euphorbia leaves (7) to attain a position (8) facing the fly just as it prepares to fly away. Presumably other pursuits were more successful than this one. The young individual was about 5 mm in length. The native P. princeps appear to thrive upon the introduced herb E. esula in northeastern North America. After Hill (1977b).

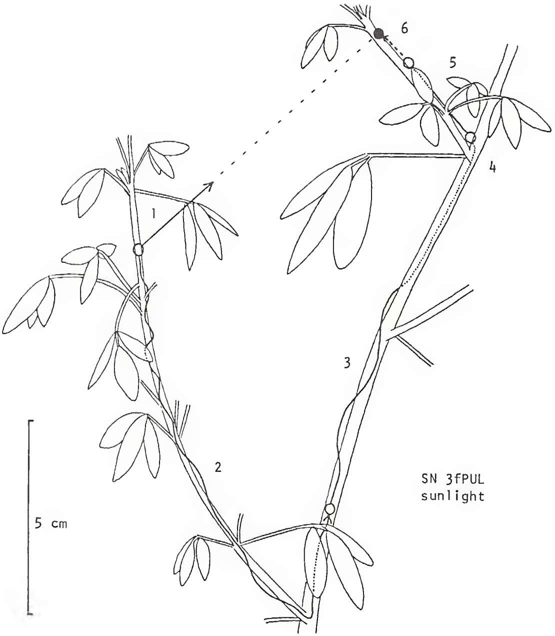


Figure 6. Indirect pursuit of an immobile (dead) fly by a female *P. pulcherrimus*. Initial movement of the fly (black spot, as in subsequent figures) leads the spider to make its initial orientation to the primary objective (1), followed by a steady, winding descent (2) to the main stem of this sweet clover (*Melilotus alba*). After a brief stop, the spider ascends steadily (3) on a winding course, stopping (4) to turn toward the completely immobile fly. A slow, step by step stalk with pedipalps flickering up and down in unison (5) is followed by a short jump and capture of the fly. This particular pursuit is somewhat unusual in its lack of intervening reorientation turns, but it does show the extent to which a *Phidippus* will backtrack to attain an otherwise inaccessible position. Since this fly was somewhat obscured by leaflets, and completely immobile during the reorientation (4), it is likely that this turn was initiated by the spider before it once again sighted the fly.

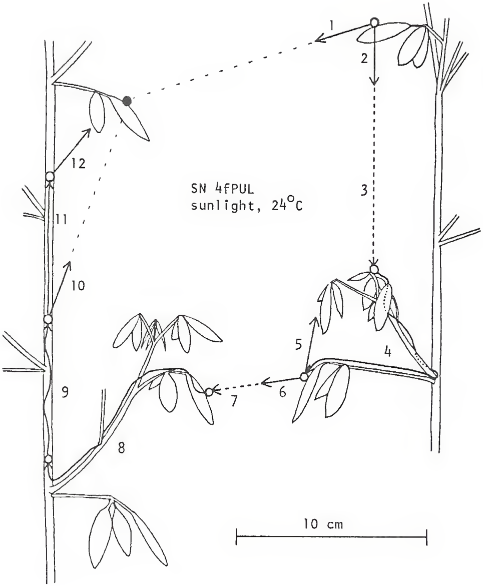


Figure 7. Indirect pursuit of fly (standard lure) on sweet clover by a female P. pulcherrimus. A standard procedure of removing the fly stimulus as soon as the spider turned away in pursuit (2) was used here. The spider orients to the fly (1), turns down (2), jumps (3), runs quickly (4), turns toward the starting position (5), turns to a nearby leaflet (6), jumps to that leaflet (7), runs quickly (8, 9), turns to leaflet where fly appeared initially (10), runs (11), and again turns to face the leaflets which may be associated with the sighted prey. The "deliberate" appearance of the entire pursuit, and particularly the turns toward the apparent objective (10, 12), suggest that the latter were real examples of reorientation in the course of a sustained pursuit. The use of a turn-down jump (2, 3) is frequently observed during an indirect pursuit. The distinction between walking and running is based solely upon a subjective impression of the velocity of the spider.

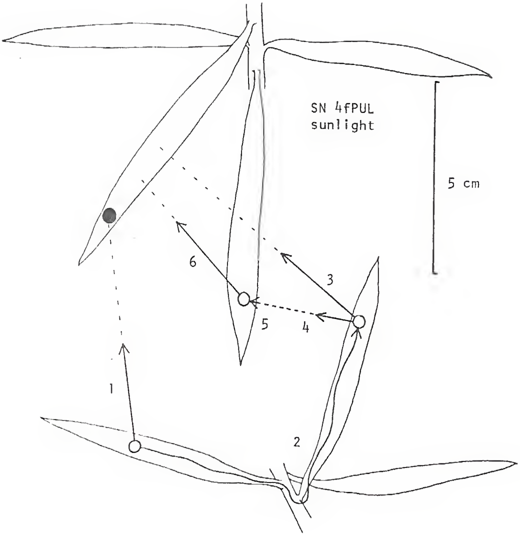


Figure 8. Indirect pursuit of fly on Solidago by a female P. pulcherrimus as viewed from above. In this situation most of the movement of the spider takes place in a single, horizontal plane; thus orientation to gravity cannot account for the ability of the spider to relocate the prey position. The dead fly is removed as the spider turns away from its initial orientation (1). Then the spider walks steadily along a route which includes several 90° turns (2), reorients to a leaf apparently associated with the primary objective (3), turns down to an accessible (nearer) leaf (4), jumps to that leaf (5), and reorients immediately to the objective leaf (6). Notice that after reorientation (3), a second segment of detour (4, 5) is utilized with no loss of orientation by the spider.

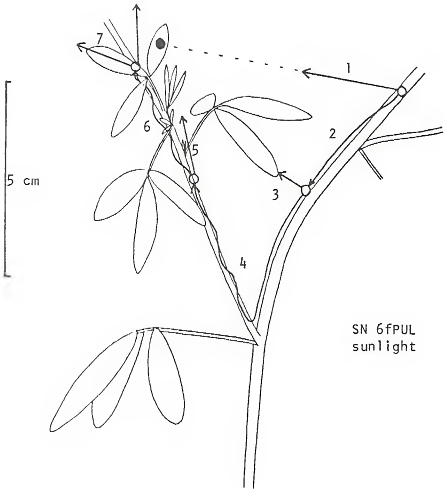


Figure 9. Indirect pursuit of sighted prey by a female P. pulcherrimus. The spider turns to the fly (1), runs (2; the fly is removed at this time), stops and attempts to reach a nearby leaflet with the forelegs, with no success after about 5 sec (3), walks steadily (4), reorients (5), walks (6), and then makes a series of small turns (7). The small turns are apparently employed for visual (AME) survey of a restricted area. Often a series of larger turns, encompassing 360°, are observed during a pause in the movement of a salticid spider. Notice that even after the distraction of reaching behavior (3), the spider maintains a memory of the prey position and continues its pursuit (4). Indirect pursuit is not a stereotyped sequence of stimuli and simple responses which can be readily disrupted by a subsequent distraction. It is better viewed as the opportunistic exploitation of potential routes of access by a spider which maintains an accurate, and persistent, memory of the primary objective.

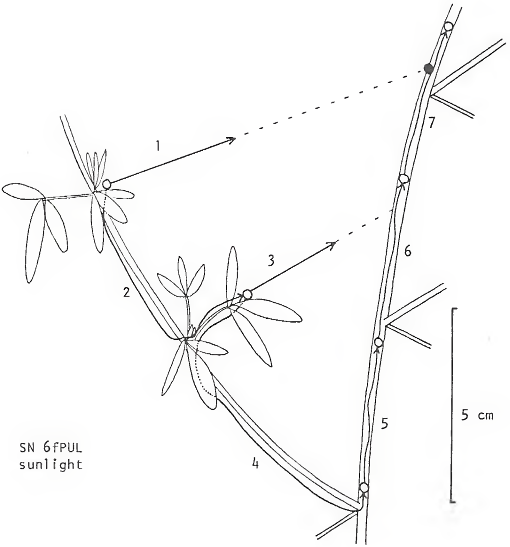


Figure 10. Indirect pursuit of sighted prey by a female P. pulcherrimus. This sequence includes the initial turn to the fly (1), a fast walk under the branch as the prey is removed (2), reorientation (3), another fast walk under the branch (4), and three (5-7) intervals of a "jerky walk" pattern of ascent. The significance of this staccato stepping pattern is not known, but the visual effect is similar to that of a hunting wasp on the prowl. The spider persists in its pursuit (4) after failing to gain access to the stem by venturing out to position (3). In a similar pursuit, another individual made a series of 4 forays out to the side branches until a position allowing for a jump to the objective plant was attained.

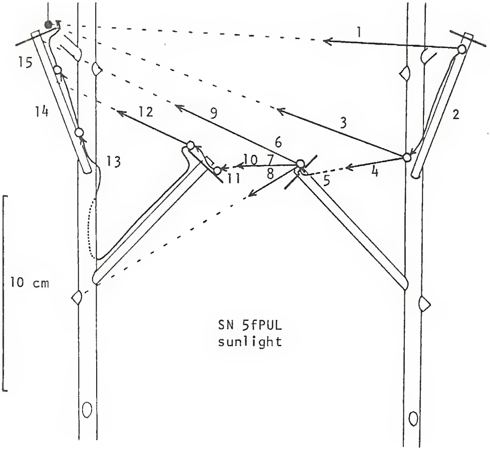


Figure 11. Indirect pursuit of sighted prey on an artificial plant (constructed with wood dowels) by a particularly adept female P. pulcherrimus. The fly was removed as soon as the spider turned away from the initial orientation (1). The sequence was then: run (2), reorient (3), turn down (4), jump (5), reorient (6), turn to green paper "leaf" at the end of a near "branch" of the objective plant (7), turn down (8), reorient (9), turn to near leaf (10), jump (11), reorient (12), fast walk (13-15). Once attaining the objective position this spider performed an extensive series of small turns. The sequence includes 4 discrete reorientations to the objective leaf (1, 3, 9, and 12), each of which initiates a new segment of pursuit. Most individuals tested did not complete this entire sequence, although they could usually get as far as reorientation (9).

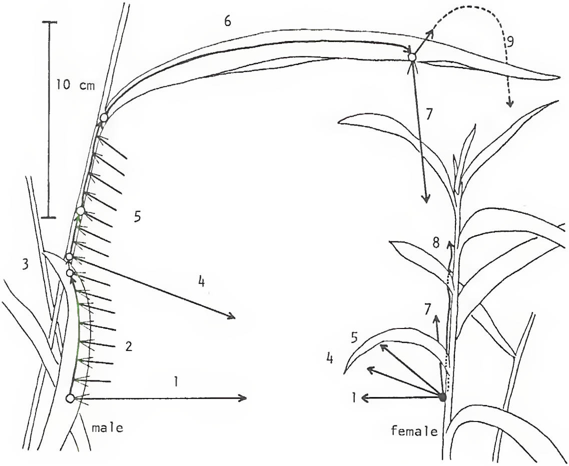


Figure 12. Indirect pursuit of a female P. audax by a male of the same species, based upon a field sketch of the event. The sequence was: (1) The male displays vigorously toward the female with legs I outstretched (note the symbolic representation above); the female faces the male. The male continues to display (2) while side-stepping and then (3) turns to jump to a grass stem. After reorientation to the female (4), which has followed the movements of the male, the male continues to display as he ascends the stem (5). After turning to run quickly over the top of a broad blade of grass (6), the male returns to the edge of the grass blade to look down from an appropriate position (7). Upon sighting the display of the male above her, the female runs in pursuit (8), and the male, in response, immediately turns around and takes a long flying leap (free-fall, no drag-line is played out) away from the pursuing female (9). The rapid escape of the male was quite adaptive in this situation, as female P. audax which have mated will never mate again, but instead they will pursue and devour the courting males whenever possible. In these circumstances, the ability of the male to retain a memory of the relative position of the female is quite as important as his ability to assess her mood. Willing females do not pursue, but wait. This fortuitous observation was made possible by an unusually high density of adult P. audax near Newnan's Lake in Alachua County, Florida during the fall of 1977.

of the surroundings. Often these spiders attain positions which were, previously, the objects of visual survey, and presumably detours are utilized for this purpose. In this study, the pursuit of prey is separated from other, more general problems of directed movement only because the presentation of prey to the spider allows one to manipulate the objectives of the spider in a controlled fashion. Actually, even within the context of a predatory pursuit, the spiders are concerned with the problem of attaining sighted plant positions which may be associated with the prey (Figures 7-11), just as they pursue secondary objectives (also plant configurations) indirectly during the course of pursuit.

In summary, the use of a detour can be viewed as an essential feature of the directed movement of Phidippus upon vegetation, and this behavior can be readily demonstrated when the spider is presented with a specific problem of prey access. Use of a detour requires both an ability to determine an appropriate route of access, and an ability to retain a memory (compensated for movement by the spider) of the relative position of the objective. This memory of prey position is frequently expressed as a reorientation turn directed toward the expected position of the prey.

SECTION VI
ORIENTATION TURNS DIRECTED TOWARD THE PREY

Salticid spiders turn to face moving objects which appear within the extensive visual field of the lateral eyes. A subsequent period of visual survey of potential prey with the front eyes (AME and ALE), which may occupy only a fraction of a second, necessarily precedes the setting of the prey position as the primary objective, or the initiation of the pursuit. As indicated in Figures 13-15, these directed turns toward visual stimuli include both α (stepping) and β (elevation of prosoma) components of movement.

Land (1971) demonstrated the ability of salticids to execute an accurate α turn to face a visual stimulus, in the absence of visual feedback (open loop; Mittelstaedt, 1962, 1964); these spiders require only the directional information provided by the initial sighting of a stimulus by a lateral eye to determine the extent of this orientation turn. In his demonstration, Land observed the stepping movement of each α turn indirectly, by measuring the angle through which a spider, affixed by the prosoma, would turn a paper ring held by the legs. Figures 16 and 17 provide an additional demonstration of the ability of untethered Phidippus to execute an accurate α turn in the absence of visual feedback from the stimulus during the course of the turn. In this demonstration, the possibility that the spider might utilize tactile information provided by the edge of a paper ring to monitor the

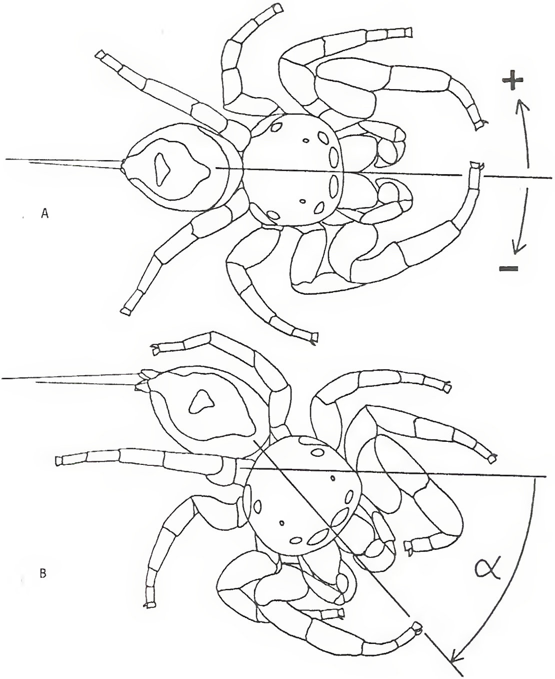


Figure 13. The α turn. Adult male *P. pulcherrimus* before (A) and after (B) completing a turn of magnitude α in the horizontal plane. The convention adopted for the sign (+ or -) of α is shown in (A). A stepping pattern like that described by Land (1972a) is usually involved in an α turn, although the spider can make small α turns in place by pivoting.

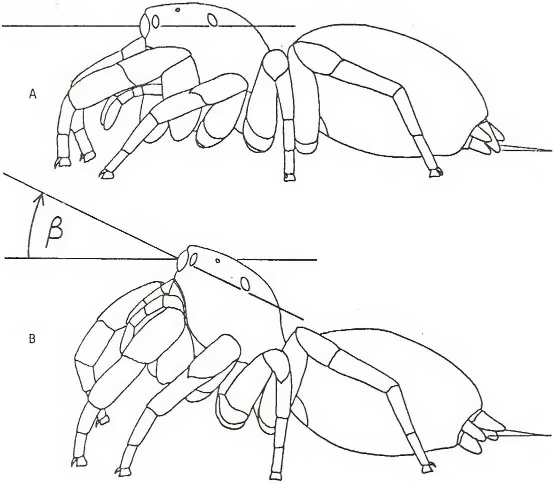


Figure 14. The β turn. *Phidippus* before (A) and after (B) completion of a rotation of the prosoma in the sagittal plane of magnitude β. Generally stepping is seldom utilized in the execution of a β turn, which involves a pivot of the prosoma upon the legs in position, to either raise (+ magnitude) or lower (-) the prosoma with respect to the substratum. *Phidippus* can turn to look directly up from a surface in this manner; by raising the pedicel above the substratum they can also lower the front of the prosoma to look down from the edge of a surface.

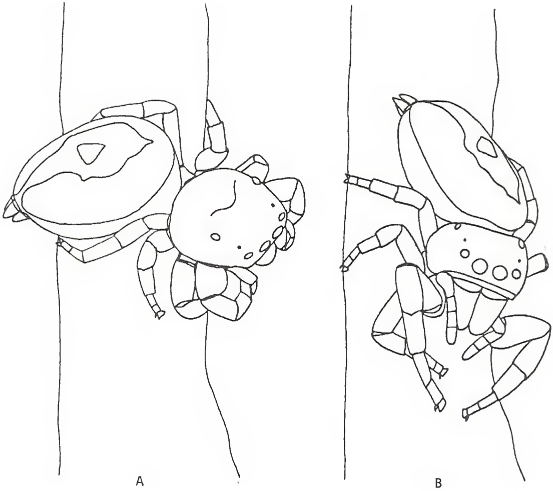


Figure 15. Smooth execution of a turn (A to B) involving both α and β components of movement by an adult female P. pulcherrimus (traced from photographs). The ability of Phidippus to execute a turn in three dimensions, involving the coordinated activity of muscles concerned with elevation of the prosoma (β), as well as those concerned with stepping upon an irregular surface (α), can be readily demonstrated by the presentation of a fly stimulus to the spider. Presentation of prey above and behind a spider resting on a horizontal surface can elicit a 180° α turn coupled with an appropriate $(+)\beta$ turn, as a single smooth movement. Often a small β correction (presumably the result of visual feedback from the prey) is required to face the prey directly, at least when the spider is resting upon a flat surface. This is related to the tendency of these spiders to turn a smaller β turn in the absence of visual feedback than is required to face the prey.

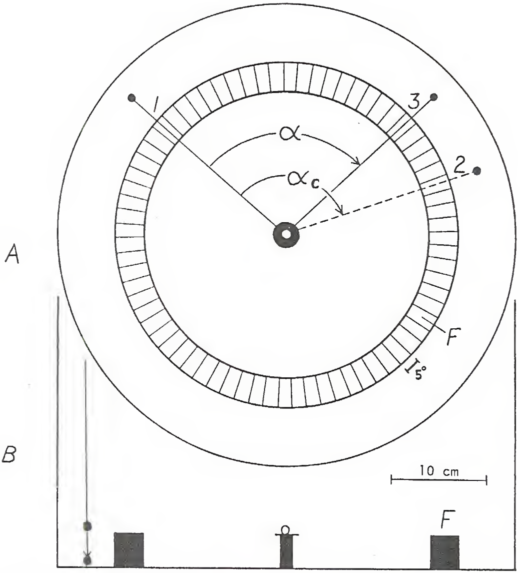


Figure 16. Apparatus used to measure the ability of untethered Phidippus to complete an accurate α turn to face prey in the absence of visual feedback, viewed from above (A), and in vertical section (B). The entire apparatus is constructed of heavy white paper. The spider (open circle) rests on a small (2 cm diameter) circular platform at the center of a large cylinder. A numbered scale (F), used to measure the direction faced by the spider, encircles the prey position. As shown in (A), the direction initially faced by the spider (1), the position at which prey appears (2), and the direction faced by the spider after the orientation turn (3) are recorded in sequence by an observer looking directly down from above the cylinder. As shown in (B), the prey (a standard lure) is dropped into the trough well before the spider has a chance to complete its turn. When there is any doubt in this regard, the trial is not recorded. From (1), (2), and (3), values of α_c, or the magnitude of α required to face the original prey position, and the actual value of α elicited by the stimulus are determined as shown in (A).

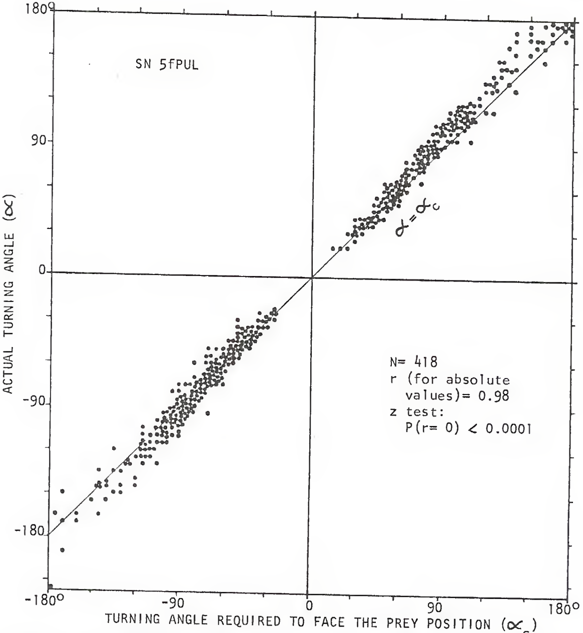


Figure 17. Data collected from a single series of trials using the technique described in Figure 16: α as a function of α_c. This female P. pulcherrimus has the ability to complete a remarkably accurate turn toward the original position of a stimulus sighted by the lateral eyes in the absence of visual feedback. Although comparable with similar results obtained by Land (1971), none of the small turns in response to a prey stimulus which he recorded have been observed. An interesting feature of this behavior lies in the fact that these spiders will always make the shortest of two possible turns toward a stimulus; where a 220° turn would suffice, the more direct -140° turn is always utilized, as an example. The accuracy of required determinations of the direction faced by the spider from a scale 15 cm distant was frequently checked by comparison of an observed orientation (by the scale) with the actual position of a fly which the spider was facing directly; the method is quite reliable, ± 5°.

extent of a turn (a potential factor in Land's demonstration, although it does not detract from his demonstration that visual feedback is not required) is not allowed. A similar demonstration of the accuracy of β turns directed toward a stimulus in the absence of visual feedback during each turn is shown in Figures 18-20; these turns consistently fall short of the stimulus position. The execution of combined α-β turns in the absence of visual feedback can also be demonstrated, but the accuracy of these turns (involving two components of direction) has not been measured.

The fact that visual feedback is not required for an accurate turn does not imply that visual feedback is not operative in non-experimental situations. Indeed, the very purpose of the orientation to prey is to allow the spider to gather additional visual information with the greater resolution and binocular vision afforded by the front eyes. If visual feedback is available, it will be utilized by the spider to direct subsequent behavior. When a second presentation of the prey stimulus, in the initial position, is made after the completion of an orientation turn executed in the absence of visual feedback by a spider on the apparatus shown in Figure 16, the spider quickly makes a second correcting turn toward the visible prey (unless the accuracy of the initial turn was sufficient). Whenever the prey remains visible during the orientation turn, the spider invariably turns directly toward the prey, although the completion of this turn often requires a small but distinct correcting turn; this correcting turn, which may be in a direction opposite to that of the original turn, is clearly the product of visual feedback. Even when running after moving prey, a Phidippus can execute a continuous series of accurate orientation turns which are

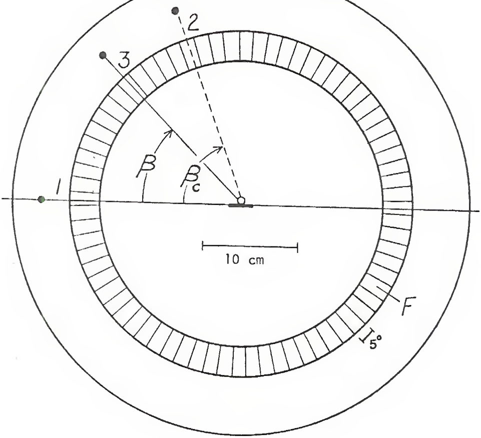


Figure 18. Apparatus described in Figure 16, after modification for the observation of β turns, as viewed from above. A 2.5 cm wide vertical platform (at center) provides a waiting position for the spider. Before each trial, the spider is shown a prey stimulus (the standard lure) at (1) to return the spider to a standard starting orientation. Following appearance of a stimulus at (2), the spider turns (3). From observed values of (1), (2), and (3), both β_c, or the turn required to face the prey position, and the actual turn (β) are determined. As in the observation of α, the fly was dropped so that it could not be employed by the spider to monitor the extent of the turn. Determination of the direction faced by the spider was consistent with the vector shown in Figure 14, as well as with the appearance of the spider when it was surveying the fly directly at position (1), above. Nonetheless it is likely that measurement of direction is less accurate here than in a situation where the spider is viewed from above.

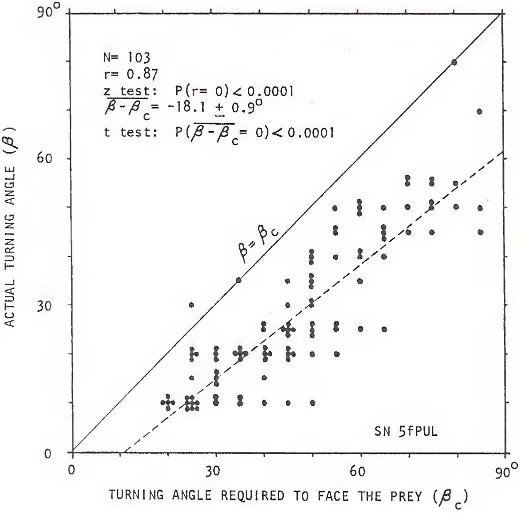


Figure 19. Performance of a female P. pulcherrimus on the apparatus shown in Figure 18. Although the angle turned by the spider correlates significantly with the angle required to face the stimulus, the angle turned is nonetheless significantly smaller than the required angle. Many of the turns shown above consisted of 2 visibly distinct β components executed in rapid succession. Subsequent presentation of prey in the initial position could often elicit an additional, small β turn (correction of the orientation to prey with visual feedback) to face the prey. In a manner consistent with the format of subsequent figures the dashed line represents the linear least-squares regression of Y (in this case β) on X (β_c).

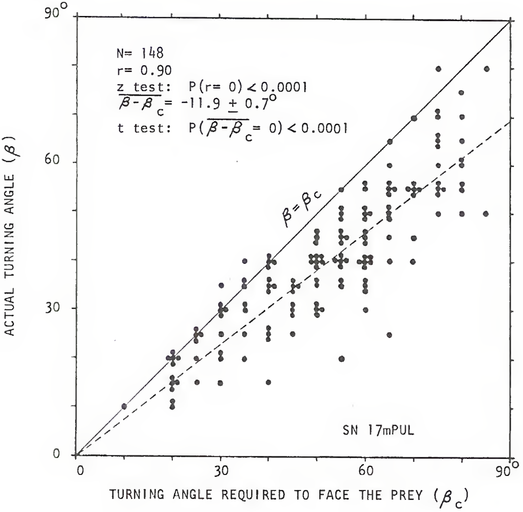


Figure 20. Performance of a male P. pulcherrimus on the apparatus shown in Figure 18. The results are consistent with those shown in Figure 19.

directed toward that prey (Figure 21). These may be closed-loop turns directed by the AME (Land, 1972b).

Salticids also appear to turn frequently in the absence of specific visual stimuli. When walking from plant to plant, both Eris (Hill, 1978) and Phidippus will frequently stop to perform an extensive (encompassing 360°) series of turns. More restricted bouts of visual survey, consisting of a series of small turns directed toward the vicinity of a particular plant configuration, are also observed; these turns are presumably directed by the AME. Salticids readily turn to face immobile objects, including prey, when these are in the field of vision of the AME.

The partial turns which Land (1971) observed in response to a directional stimulus probably correspond to these small survey turns. These incomplete turns have not been observed in response to a specific directional stimulus in any of the experimental situations utilized in the course of this study. Extensive field observations of both Eris and Phidippus suggest that there is no real basis for Land's attempt to justify these partial turns in terms of energy conservation by the spider; salticids turn frequently, and most of their turns are directed toward inanimate objects, such as leaves blowing in the wind. Partial turns in response to specific directional stimuli are not observed, as a rule.

Many features of the orientation turn are shared with the reorientation turn characteristic of the indirect (detoured) pursuit. In both cases the turn is directed toward the expected position of prey as accurately as possible, and both turns involve the simultaneous (or, in some cases, sequential) completion of both α and β components of

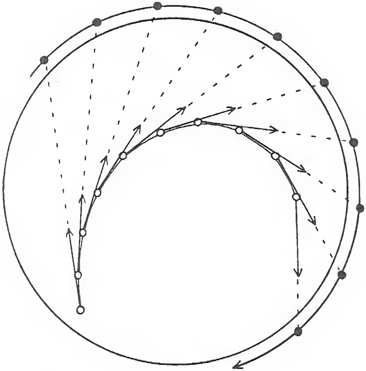


Figure 21. This diagram shows the approximate relationship of spider (open circles) to prey (solid dots) positions during a running pursuit of the moving prey. Phidippus can continuously orient to the moving prey during its own movement. Stepping patterns involved in the movement described above must include integrated components of both forward movement (taxis) and turning (orientation). Observations of the ability of Phidippus to capture moving prey suggest that these spiders may continuously orient to a position in front of the moving prey in a situation like this.

movement, generally integrated into a single, smoothly executed turn. In addition, the accurate completion of both orientation and reorientation turns requires an ability of the spider to account for the relative starting positions of the components of its own body (proprioception, or kinesthesis) in determining the appropriate motor output. In the absence of visual feedback, proprioceptive feedback is presumably required to monitor the extent of these directed turns.

SECTION VII
CRITERIA FOR PURSUIT

Subsequent to the completion of an orientation turn toward a particular stimulus, the salticid is in a position to evaluate the object of its attention with the high resolution provided by the AME, in addition to information provided by the ALE. The movement, size, and form of potential prey all affect the probability of pursuit (Plateau, 1887; Heil, 1936; Drees, 1952; Gardner, 1966; Land, 1971; Dill, 1975). Features of either the behavior or appearance of prey can be important determinants of the specific response of the spider as it approaches that prey: At a distance of 1.5 cm, a stalking *Evarcha* will subsequently avoid a bee, jump upon a fly, or subject a beetle to extensive tactile exploration (Dahl, 1885). *Salticus scenicus* will stalk after slowly moving prey, but they will run if the prey is moving quickly (Drees, 1952); prey mobility may also be a factor in the approach of *Phidippus regius* to prey (Edwards, 1975). Araneids possess an innate (not learned) versatility in their handling of prey (Robinson and Robinson, 1976), and it is likely that much of the versatility in the approach of salticids to various types of prey is also subject to genetic determination.

The experience of the spider may also be a critical determinant of subsequent behavior. Salticids can learn to alter their response to a particular type of prey for an indefinite period after a disagreeable encounter (Drees, 1952). Gardner (1964, 1966) found that *Phidippus* are more responsive to prey after longer periods of food deprivation. Satiated Phidippus tend to lose their interest in the pursuit of prey. Salticids will run only a limited number of pursuits in a given situation, a result which has been ascribed to the fatigue of a particular hunting instinct (Drees, 1952; Precht and Freytag, 1958; Gardner, 1964; Dalwigk, 1973). However, Plett (1975) found that recovery to this "fatigue" was stimulus-specific, and the waning performance of a spider could be considered a temporary acceptance of the futility of a particular form of action.

This interpretation of fatigue is consistent with the predatory behavior of Phidippus observed in the laboratory. Individuals which will no longer pursue a prey at the distance of 25 cm if this pursuit would require a detour, will readily pursue the same prey at the same distance if the route of access is direct. This applies to individuals which had previously demonstrated an ability to negotiate the detoured approach without any difficulty. Other individuals may not move from a waiting position unless the prey remains in position, or immobile, for a period which may exceed 15 sec.

Therefore, and admittedly in the absence of conclusive data, it is proposed that the prey distance, the position of the prey relative to a route of access visible to the spider, and the duration of prey immobility are all factors which, in combination with the experience and innate disposition of the individual spider, determine the probability of pursuit in a given situation. Much of the behavior of Phidippus subsequent to the initial orientation turn to face a potential prey can be interpreted, in a functional sense, as the evaluation of the feasibility (or futility) of pursuit. When the prey appears in a position which is readily accessible, the spider may pursue without hesitation. As noted above, a lengthy waiting period may precede the initiation of a detoured pursuit. This waiting period, although it may be of use for the evaluation of potential routes (see below), may also serve to measure the probability that the prey will still be in its position when the spider, after some effort, has attained that position. This would be true if the probability that a prey will remain in position for a particular interval of time correlates positively with the probability that it will remain in position for the subsequent interval. If prey tend to alight and then take off quickly, a lengthy pursuit is wasted effort. This appraisal requires at least a generalized ability on the part of the spider to assess the effort required for the completion of a detour, an ability which is consistent with the imperative role of vision in the selection of a detour by the spider.

In a more general sense, this hypothetical versatility agrees with the observed ability of Phidippus to conduct a directed search when prey are sedentary, as mentioned earlier. It appears that these spiders can adjust their behavior to account for the mobility of the available prey, in determining an effective strategy of predation.

SECTION VIII
SELECTION OF THE ACCESS ROUTE

Salticids use vision to evaluate objectives and objective positions. In a corridor, salticids of the genera Evarcha, Heliophanus, Marpissa, Salticus, Sitticus, and Synageles will move toward a striped wall in preference to an unmarked wall (Kästner, 1950; Dzimirski, 1959). In Figure 22 a similar demonstration of the role of vision in determining a direction of movement by Phidippus is presented. One significant feature of the ascent shown in this figure is the tendency for this spider to stop and conduct an extensive visual survey whenever the ascent is interrupted (decision points). The visual determination of an objective, which in this case is clearly a vertical rod in the context of ascent, consistently precedes movement in a horizontal plane from each decision point. Salticids do not grope blindly in space when visual information is available, but move under the direction of specific objectives.

Figures 4 (B, E) and 23-26 (corresponding to data given in Tables 2-4) provide several different demonstrations of the role of vision in the selection of a route of access to the prey position. As noted earlier, the determination of the immediate direction of pursuit is related in each case to the relative position of a plant configuration which is part of the total route of access. This configuration is termed the secondary objective, since it replaces the primary objective (prey) as a determinant of immediate behavior.

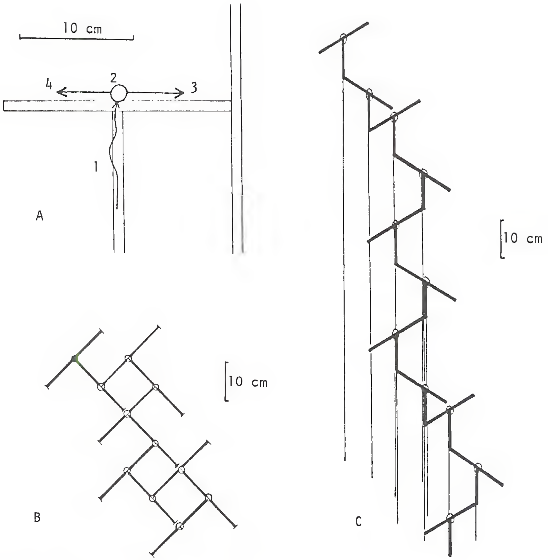


Figure 22. Sequential T-maze problem. The individual T, constructed of wood dowels, is shown in (A): The spider ascends (1) to a decision point (2), then either moves toward the visible route of ascent (3) or in the opposite direction (4). The structure shown in both horizontal plane projection (or view from above; B) and lateral perspective (C), provides the ascending *Phidippus* with a series of 10 consecutive T choices during each ascent. Each of the 10 decisions occurs at a level 10 cm above the level of the preceding decision. In a total of 10 ascents upon this structure, a single male *P. pulcherrimus* (SN 7mPUL) moved in direction (3) as indicated in (A) in 97/100 choices ($P < 0.001$). In each trial this spider completed a steady walk to the top of the structure. Pauses for visual survey always occurred at the decision points, indicated by open circles above. The same individual completed a run to the top of this structure in the dark (as observed by faint red illumination from below), but in this case only 4/10 of its decisions were directed toward the route of ascent, and there was no pause for visual survey prior to a decision. In all cases the spider walked on *top* of the horizontal bars.

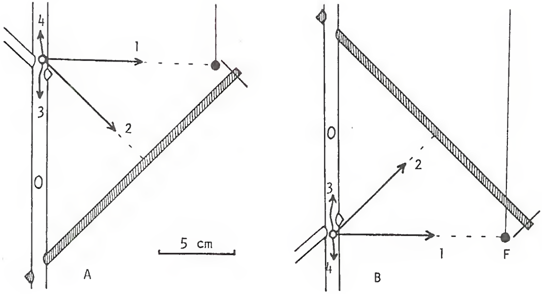


Figure 23. Demonstration of the role of vision in the determination of a route of pursuit, irrespective of gravity. Each problem can be repeated at a series of positions on an artificial plant constructed of wood dowels. Both problems (A) and (B) begin with the presentation of the standard lure (hanging dead fly) to the spider as shown (F). The spider (open circle on main stem) immediately turns to face the fly (1), to initiate the trial. It should be noted that the relative situation of the prey in a horizontal direction perpendicular to the vertical main stem on which the spider rests is the same in both problems; the critical difference, then, is the relative position of the physical connection (shaded) between the main stem and the position of the fly. The spider is lured into an appropriate starting position with the fly, prior to each trial. Pertinent data includes the number of trials in which a distinct orientation toward the access route (2) is observed, the number of trials in which the spider moves toward this access route (3; this requires a descent in A, and an ascent in B), and finally the number of trials in which the spider turns away from the access route, to move either up (A) or down (B) the stem after sighting the prey (4, above). If vision were a significant determinant of the direction of pursuit, one would expect event (3) to occur significantly more often than event (4), in both problems. This expectation agrees with the actual results (Table 2).

Table 2. Results pertaining to the access problems (A) and (B) as they are presented in Figure 23.

PROBLEM A: DESCENT REQUIRED FOR ACCESS

SN	N	2.Distinct turn to route (N_2)	3.Run down to route (N_3)*	4.Run up (N_4)	$P(N_3 = N_4)$
1fPUL	30	19	29	1	< 0.001
3fPUL	22	16	20	2	< 0.001
5fPUL	20	2	20	0	< 0.001
7fPUL	4	1	4	0	-
total PUL	76	38	73	3	< 0.001
22fREG	40	31	33	7	< 0.001
24fREG	15	14	15	0	< 0.001

*In some cases, a direct jump down to the access route.

PROBLEM B: ASCENT REQUIRED FOR ACCESS

SN	N	2.Distinct turn to route (N_2)	3.Run up to route (N_3)	4.Run down (N_4)	$P(N_3 = N_4)$
1fPUL	22	10	22	0	< 0.001
3fPUL	32	13	32	0	< 0.001
4fPUL	6	0	6	0	-
5fPUL	38	5	38	0	< 0.001
6fPUL	22	3	22	0	< 0.001
total PUL	120	31	120	0	< 0.001
22fREG	44	1	44	0	< 0.001
24fREG	64	3	64	0	< 0.001

The numbered column headings (2-4) correspond to events described in Figure 23. Both P. pulcherrimus (PUL) and P. regius (REG) were observed. Clearly, as shown by chi^2 analysis of these enumerative data (column at far right), the decision to either ascend or descend is based upon the relative position of the access route, which may be termed a secondary objective. Although distinct turns toward the route of access are not observed in most of these trials, prior to the initiation of pursuit, this decision is clearly the result of visual evaluation of the relative position of the access route; thus this process is complete in most cases before the spider even turns away from the prey, in this particular problem. In every case of ascent (4) in problem (A), the spider moved up the stem to position for a direct jump toward the prey.

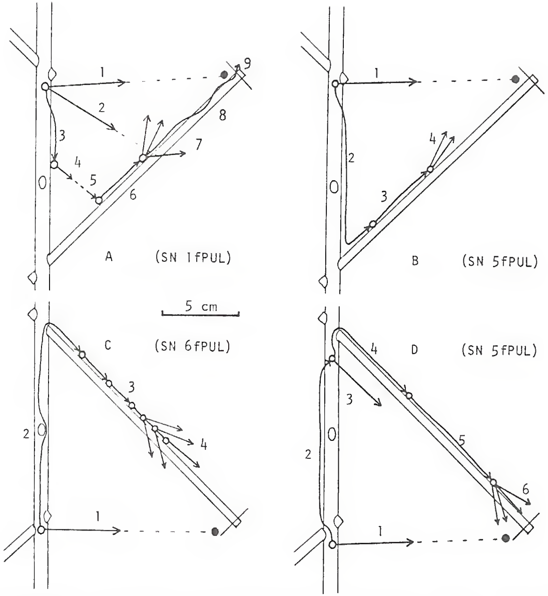


Figure 24. Some typical solutions to the problems of access presented in Figure 23. In each case the fly was quickly removed with no effect on the spider as soon as the spider turned away from the initial orientation to run a pursuit. Thus the subsequent pursuit is not dependent upon a continuing prey stimulus. A: The spider turns to face the prey (1), turns down to the access route (2), runs down on the side of the stem facing the access route (3), turns (4), and jumps (5) to the secondary objective, ascends (6), stops for a series of small turns (7), ascends (8), and finally (9) explores the apical region (green paper "leaf") of the branch. B: Typically for this individual, the initial orientation (1) is followed by a fast walk (2) directly toward the access route, then ascent (3) and small turns (4). C: Turn to prey (1), fast walk (2), halting descent (3), and interrupted small turns (4). D: Turn to prey (1), slow walk on side of stem opposite to the prey direction (2), reorientation (3), walk (4, 5), and small turns (6).

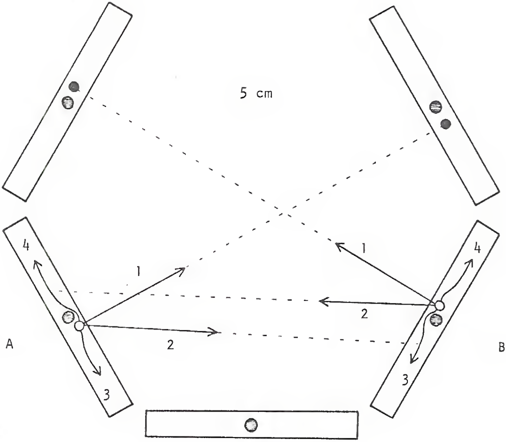


Figure 25. Demonstration of the visual determination of the access route on a "circle of plants," as viewed from above. Each long rectangle is a green paper "leaf," skewered (at center) by a long vertical wood dowel (stem). Problems (A) and (B) are run alternately for the most part. In each trial the spider first turns to face the prey (standard lure; 1). As in the preceding experiment (Figure 23), distinct turns toward the connecting segment of the access route (2), and the subsequent direction of movement by the spider (3 or 4) are recorded. The hypothesis of visual determination requires that event (3), or movement toward the continuous access, occur significantly more often than the alternative (4). Results which are consistent with this hypothesis are presented in Table 3.

Table 3. Results for the problems of access presented in Figure 25.

SN	N	2. Distinct turn to route (N_2)	3. Run toward access (N_3)	4. Run away from access (N_4)	$P(N_3 = N_4)$
1fPUL	24	22	24	0	< 0.001
3fPUL	37	24	37	0	< 0.001
5fPUL	5	5	5	0	-
22fREG	70	45	60	10	< 0.001
23fREG	42	3	41	1	< 0.001

Since a comparable number of trials was run for each of the two mirror-image problems described in Figure 25, with no significant difference in the results, data for problems (A) and (B) are pooled in this table. The numbered column headings correspond to events described in Figure 25. Individuals of both species (P. pulcherrimus and P. regius) exhibit a highly significant tendency to move in the direction of the visible route of access. In this situation, most individuals make a distinct turn (2) toward the connecting route (or plant) before turning to run the pursuit, in a majority of their trials.

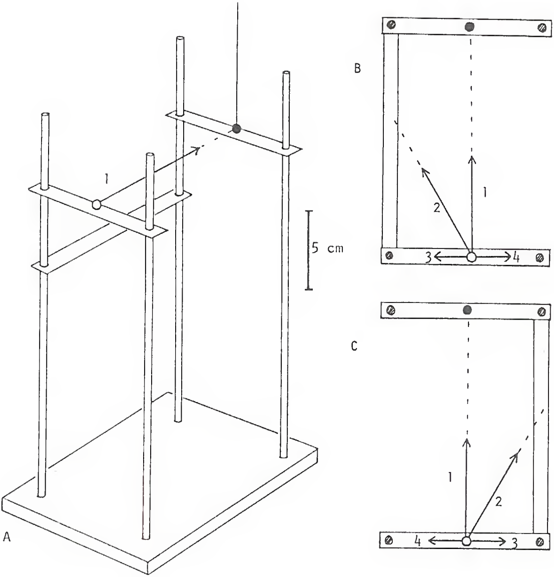


Figure 26. Problem of access requiring the use of a connection which is removed from the plane defined by the immediate route and the prey position. This problem is shown in perspective (A), and also as both left- (B) and right-handed (C) configurations, as viewed from above. As with the preceding problems, turns directed toward the connecting route (2), as well as the direction of movement (3 or 4) from the starting position, after the initial orientation to the prey (1), are recorded for each trial. Since data obtained for either of the two possible configurations of this problem are comparable for each of the individual spiders, these data are pooled in Table 4.

Table 4. Results for the problem of access in three dimensions which is described in Figure 26.

SN	N	2. Distinct turn to route (N_2)	3. Run toward access (N_3)	4. Run away from access (N_4)	$P(N_3 = N_4)$
1fPUL	41	41	41	0	<0.001
3fPUL	40	40	40	0	<0.001
22fREG	38	30	34	4	<0.001
25mREG	40	34	35	5	<0.001

The numbered column headings correspond to events described in Figure 26. Each spider has not only a highly significant tendency to move in the direction determined by the connecting route of access, but also a significant tendency to turn directly toward that connection most of the time before pursuit. Each turn toward the secondary objective (2) is quite distinct. The two female P. pulcherrimus repeatedly ran the problem in either direction like clockwork, never missing a distinct turn toward the access route prior to pursuit. This contrasts somewhat with the results of the two preceding experiments, where such turns were often omitted by the same individuals. In this problem, however, the connection between the access route and the immediate route is more complicated. All of the features relevant to the solution of this problem are not coplanar.

In a substantial majority of the access problems presented to various Phidippus during the course of this study, the spiders almost invariably utilized the most direct route of access to the prey that was available. One might think that a considerable amount of insight is required to acheive this particular result, but it is actually easier to explain this efficiency with a simple evaluation of the constraints in the spider's choice of a direction of movement upon the plant. A stem, for example, allows for only 2 directions of movement. A simple rule for behavior in choosing a direction of movement on a stem during the pursuit of prey can be stated: Move in a direction which forms an acute angle with the direction of the prey. This basic rule is an effective predictor of the behavior of Phidippus on a simple, isolated runway in a horizontal plane; here compliance with the rule invariably leads the spider to the closest possible approach to that prey. Nonetheless, this "rule" is clearly violated by the spider in many situations, including the problems of access shown in Figures 23 and 26.

These apparent violations of the acute angle rule can be reconciled with that rule, given a new understanding of the role of the secondary objective. Any objective (primary or secondary) can be viewed as a determinant of the behavior of the spider with respect to the choices offered by the immediate route, in a manner consistent with the acute angle rule given above. During each segment of pursuit, the spider is in compliance with the acute angle rule in moving toward its immediate objective; the rule can be stated in a more general form: Move in that direction (afforded by the immediate route) which forms an acute angle with the direction of the immediate objective. In this form the rule actually provides a functional definition of the term objective. The ability of Phidippus to solve a complicated problem of access is dependent upon its ability to substitute intervening, or secondary, objectives for the primary objective, as determinants of immediate behavior.

A fundamental question, then, is the nature of the visual relationship between the prey position and another position in space, which determines the role of the latter as a secondary objective. Clearly the secondary objective should be selected on the basis of its ability to afford access to the prey position. With a slight rephrasing, the acute angle rule can also be applied with some predictive value here: Provided that it is not too far away, move toward a secondary objective which is situated in a direction which forms an acute angle with the direction of the prey. Then, if direct movement toward the secondary objective is not possible, the acute angle rule can be applied to predict the direction of movement on the immediate route toward the secondary objective. If several potential secondary objectives are available, then the spider might simply move toward the first sighted position which meets certain criteria.

Certainly the pursuit behavior of Phidippus involves a more versatile approach to the problem of access than one can describe with a simple rule. As shown in Figure 27, the route of access which is employed by Phidippus does not necessarily consist of a visible plant configuration. Jumping routes and lines of silk can also be utilized. Certain features of individual behavior are best explained by their contribution to the concealed approach of the spider. As noted by Holling (1966), a direct route selected for purposes of speed may

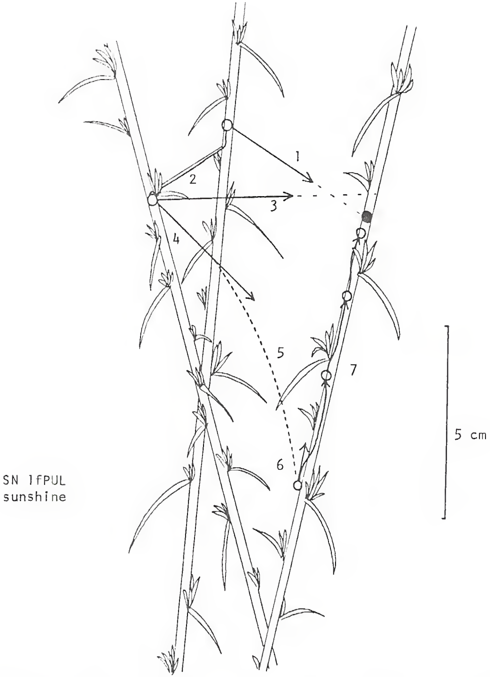


Figure 27. Use of a dragline and a jump to complete a route of access, by a female P. pulcherrimus. After the initial turn to face the prey (1), the prey (standard lure) is immediately removed. Subsequently, the spider locates and climbs under an existing dragline (2), reorients (3), turns down toward the plant associated with the primary objective (4), jumps down (5) and recovers (6) to ascend the objective plant in a series of short runs (7).

conflict with the advantages of concealment during an approach to a particular type of prey. As shown in Figure 24 (D), certain spiders would consistently climb up the opposite side of the stem from the prey direction, during each pursuit which required an ascent. Many individuals only behaved in this manner on occasion. The fact that this behavior is part of the repertoire of at least *P. clarus* and *P. pulcherrimus*, once again suggests the versatility of *Phidippus* in selecting a strategy which may be appropriate for certain prey under certain conditions. *Phidippus* consistently *descend* a vertical stem on the side facing either the primary or the secondary objective.

In summary, *Phidippus* can set a series of immediate objectives, beginning with the position of the prey (primary objective), during the course of pursuit. Selection of secondary objectives presumably relates to their position with regard to the primary objective, in terms of access to the primary objective. This selection can be the result of visual evaluation of the problem of access by the spider. The behavior of the spider on its immediate route is consistent with the pursuit of the immediate objective; by moving in a direction which forms an acute angle with the direction of the immediate objective, the spider approaches that objective as directly as possible. The use of a series of secondary objectives can lead the spider to utilize the most direct route of access that is available in many situations.

As noted earlier, the additional ability to maintain a memory of the relative position of the prey at all times during pursuit is as essential as the ability to pursue appropriate secondary objectives. A long pursuit may consist of a series of segments, each initiated by a reorientation to the expected position of the prey. After each reorientation to the prey, the spider may select a new secondary objective, or immediate destination. Thus the choice of an appropriate secondary objective during each segment of pursuit depends ultimately upon the accuracy of the spider's ability to remember where the prey is located.

SECTION IX
ORIENTATION WITH REFERENCE TO THE DIRECTION OF THE IMMEDIATE ROUTE (θ ORIENTATION)

Of all the potential references which might be employed by Phidippus in the determination of a direction in space, the orientation of the body axis itself is the most immediate. In orienting toward sighted prey in the absence of visual feedback, as described above, these spiders are in effect utilizing the orientation of the prosoma in space (corresponding to the positions of the eyes) as a reference direction for the execution of an appropriate directed turn. In a broader sense, the immediate route of the spider can also provide a very useful reference direction during the pursuit of prey. Basic terms which are used in the description of a simple segment of pursuit are presented in Figure 28. Angles which specify a particular direction with reference to the direction of a route are denoted as θ; hence the orientation of these animals with reference to the direction of the immediate route is termed θ orientation.

Figures 29 and 30 provide a description of the apparatus used to measure the ability of Phidippus to utilize θ orientation during a segment of pursuit on a horizontal route. As shown in Figure 30, this apparatus allows for the measurement of orientation and reorientation angles in a horizontal plane. The arrangement and conduct of this experiment effectively eliminate most visual cues which might be employed in the determination of a direction of reorientation by the

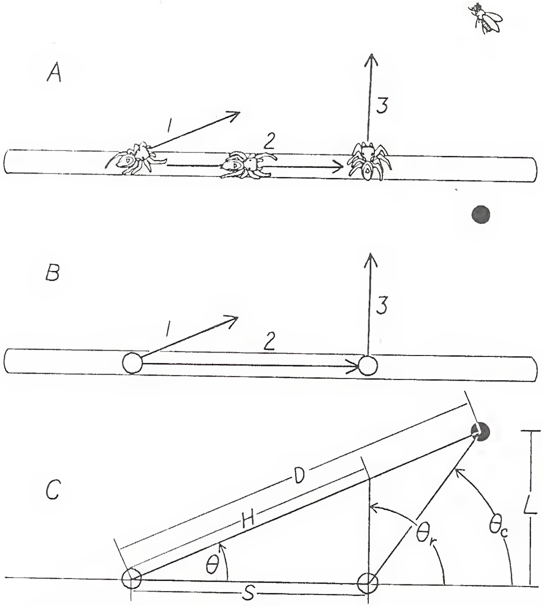


Figure 28. Direct (A), symbolic (B), and analytical (C) diagrams of a segment of pursuit on a horizontal bar. A, B: The spider turns to face the prey (1), turns away to run a segment of pursuit (2), and then reorients (3). C: Definition of terms used to describe this behavior. θ is the angle between the original spider-to-prey vector (magnitude D) and the pursuit vector (magnitude S). θ_r is the observed reorientation angle with reference to the direction of pursuit; θ_c is the calculated value of θ_r which would bring the spider to face the original prey position. θ_c is a function of θ, S, and D. H is the distance estimate of the spider which is implicit in the determination of θ_r; H is a function of the measured values of θ, S, and θ_r. L is the distance between the prey and the route of access.

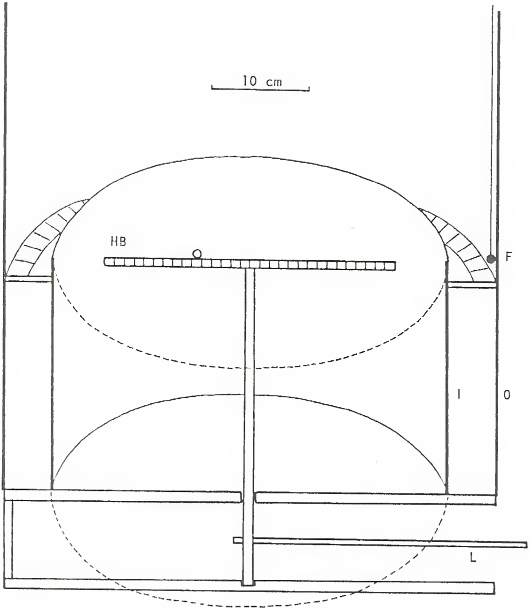


Figure 29. Vertical section of apparatus used to measure pursuit behavior on the horizontal bar, with some added perspective. The spider (open circle) runs on the horizontal bar (HB) at center, a wood dowel 9 mm in diameter. The bar is surrounded by an inner (I) and an outer (O) cylinder of heavy white paper. A lever (L) permits rotation of the bar in a horizontal plane. The standard lure (F) can be dropped into a trough between the two cylinders, out of sight of the spider, at the beginning of each pursuit. A hanging incandescent lamp is centered above the apparatus. The top of the horizontal bar is level with the top of the inner cylinder.

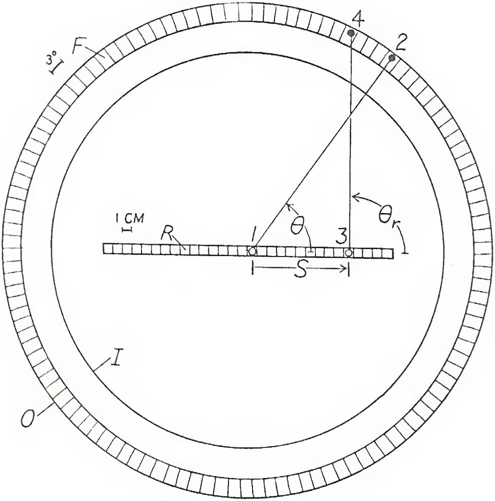


Figure 30. Horizontal bar within inner (I) and outer (O) white paper cylinders, as viewed from above (see also Figure 29). Prior to each run, the spider is led back to a center position (1) on the horizontal bar with the standard lure, to maintain a constant prey distance (D) at the initial sighting. The prey (standard lure) is presented to the spider in a circumferential position (2). Subsequently, as the prey is dropped out of sight of the spider, the spider runs to a new position on the horizontal bar (3) and reorients in the direction of position (4) on the circumferential (F) scale. From values 1-4, θ, S, and θ_r are determined. θ_c is also calculated for each pursuit, as it is defined in Figure 28. Running (R) and circumferential (F) scales are divided into 1 cm and 3^o units respectively, as shown above. For each pursuit the values 1-4 are read in sequence by an observer lookin down from above. The accurate determination of (4) requires the most critical attention on the part of the observer.

spider, apart from those provided by the route itself. In addition, gravity is of no use for the determination of a direction in the horizontal plane.

The results of this experiment are given in Figures 31-38. For each series of trials, involving the presentation of prey at varying directions with reference to the horizontal bar (variable orientation angle, θ), the measured angle of reorientation with reference to the route (θ_r) is presented first as a function of θ (Figures 31, 33, 35, and 37), and then as a function of θ_c (Figures 32, 34, 36, and 38), as the latter is defined in Figure 28. From this presentation it is possible to draw several conclusions. First, for each of the individual spiders (including P. pulcherrimus, P. clarus, and P. princeps), the actual reorientation angle (θ_r) correlates quite significantly with, and approximates somewhat, the initial orientation angle (θ). θ_r is clearly a function of θ.

In addition, θ_r tends to be significantly greater than θ in magnitude. This is demonstrated by the fact that, for each spider, $\overline{\theta_r - \theta}$ is significantly greater than 0. The graphic presentation of θ_r as a function of θ (Figures 31, 33, 35, and 37) provides a clear exhibition of this fundamental result. From an examination of Figure 28 (C), one can see that the expected value of θ_r, if it were compensated for the relative movement of the spider, should exceed the value of θ. As the spider approaches the prey (Figure 28), the reorientation angle required to face the prey position directly (θ_c) increases. From the data presented in Figures 32, 34, 36, and 38, it is evident that θ_c is an effective predictor of the measured reorientation angle (θ_r).

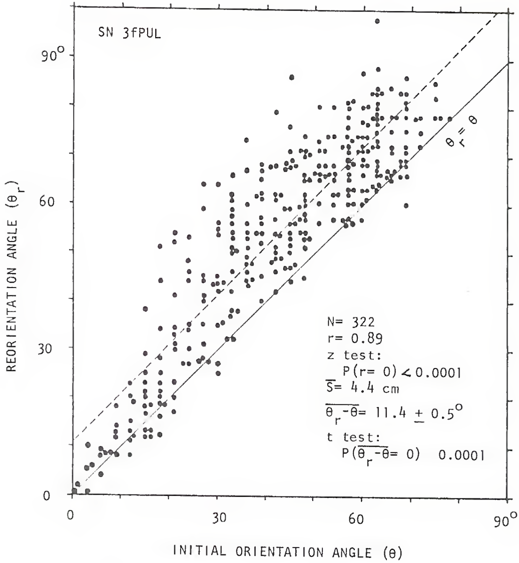


Figure 31. Behavior of a female *P. pulcherrimus* on the horizontal bar: the measured reorientation angle with reference to the direction of pursuit (θ_r) as a function of the initial orientation angle (θ). There is no doubt that the magnitude of the reorientation angle is strongly correlated with the magnitude of the orientation angle; θ_r is also significantly larger than θ. As a standard procedure in this and subsequent figures, the linear regression of Y (θ_r) on X (θ) is indicated as a dashed line.

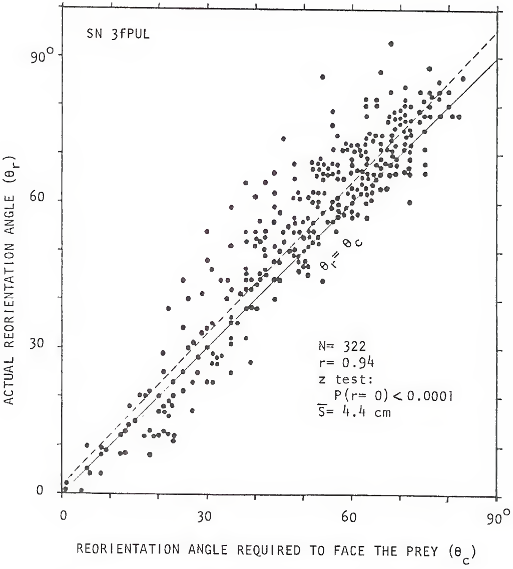


Figure 32. Behavior of a female P. pulcherrimus on the horizontal bar: θ_r as a function of θ_c, same data shown in Figure 31. As indicated by the linear regression (dashed line), θ_c is a good predictor of the measured values of θ_r. As shown in Figure 28 (C), θ_c is the reorientation angle which would bring the spider to face the original prey position directly after movement of magnitude S; it is a function of θ (initial orientation angle), S, and D (initial prey distance).

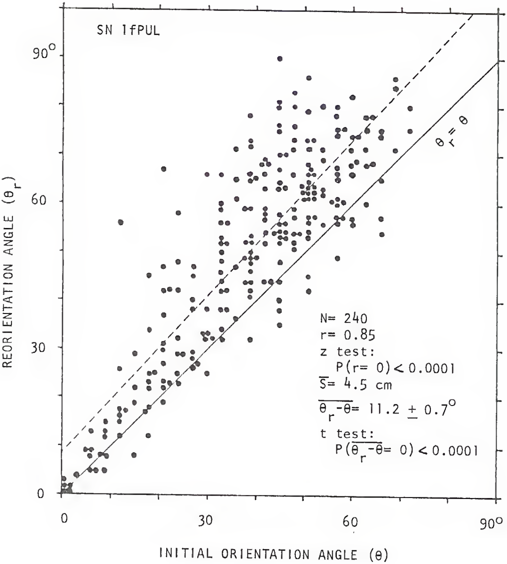


Figure 33. Behavior of a female P. pulcherrimus on the horizontal bar: θ_r as a function of θ. As for the data presented in Figure 31, the correlation of θ and θ_r is highly significant, and θ_r is significantly greater than a corresponding θ.

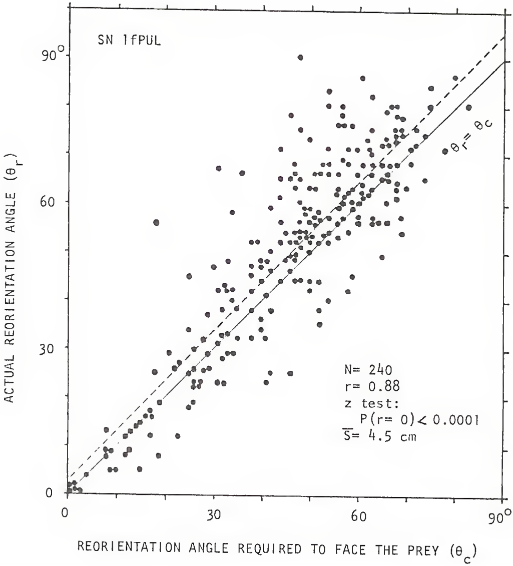


Figure 34. Behavior of a female *P. pulcherrimus* on the horizontal bar: θ_r as a function of θ_c. The analysis of these data is consistent with that presented in Figure 32.

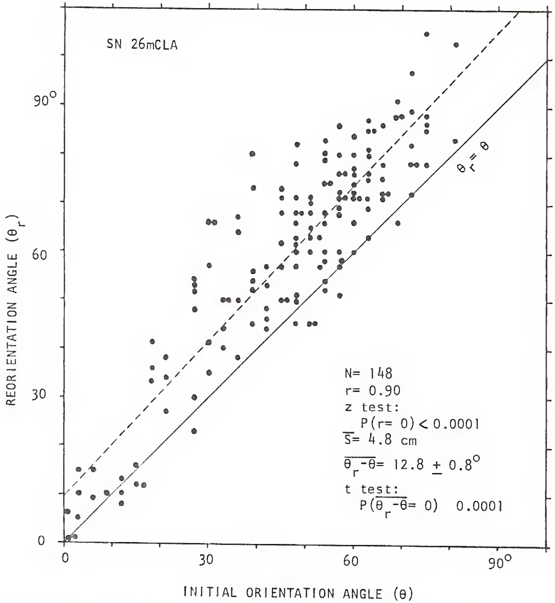


Figure 35. Behavior of a male *P. clarus* on the horizontal bar: θ_r as a function of θ. Analysis of these data is consistent with that presented in Figure 31.

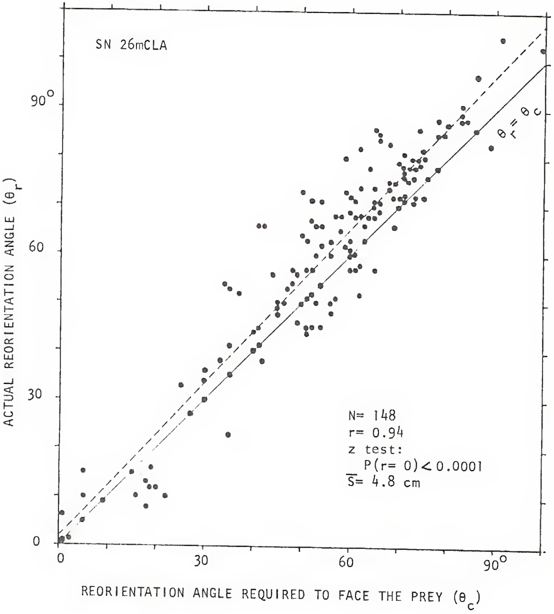


Figure 36. Behavior of a male P. clarus on the horizontal bar: θ_r as a function of θ_c. The analysis of these data is consistent with that presented in Figure 32.

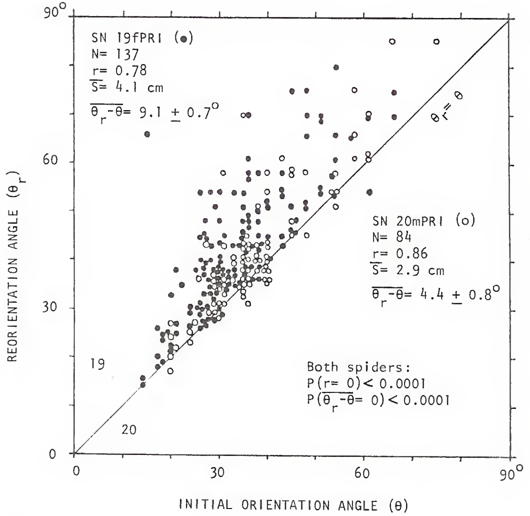


Figure 37. Behavior of a male and a female P. princeps on the horizontal bar: θ_r as a function of θ. These data were collected on the modified horizontal bar as shown in Figures 48 and 49. The numbers (19) and (20) demarcate the linear regressions for the two spiders, by number. Analysis of these data is consistent with that presented in Figure 31.

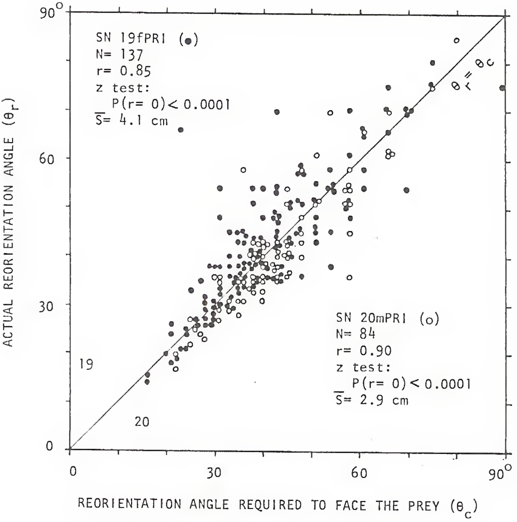


Figure 38. Behavior of a male and a female P. princeps on the horizontal bar: θ_r as a function of θ_c. The numbers (19) and (20) demarcate the linear regressions for the two spiders, by number. Analysis of these data is consistent with that presented in Figure 32.

It is evident that each reorientation turn represents an attempt by the spider to face the expected position of the prey. Within the context of some reference system, Phidippus can definitely remember the relative direction of the prey, as shown by the accuracy of the reorientation turn. The close relationship between the measured value of θ_r and the calculated θ_c for a given pursuit suggests that, if the spider is actually using the direction of movement as a reference direction (memory constitutes use of θ information), then it may also be able to compensate for its own displacement during pursuit (of magnitude S) in determining an appropriate reorientation [since $\theta_c = f(\theta, S, D)$]. Therefore a more rigorous demonstration of the role of the route, or the immediate direction of movement, in determining a direction of reorientation would be useful.

Such a demonstration is provided in Figures 39-41. When the horizontal bar is rotated by 90° during the course of pursuit, the spider still reorients according to the reference direction provided by the direction of its movement upon the bar, irrespective of the rotation of the bar, and apparently in preference to conflicting data from background visual cues available in an open room. In addition, as shown by the data presented in Figures 42 and 43, this reorientation behavior (with θ_c as an accurate predictor of θ_r) does not depend on any visual feedback in its execution. After the initial orientation to prey, Phidippus can complete a segment of pursuit, followed by an accurate reorientation turn, in complete darkness.

As shown in Figure 44, even second reorientations in response to a single stimulus follow θ_c, or θ, with an appreciable accuracy.

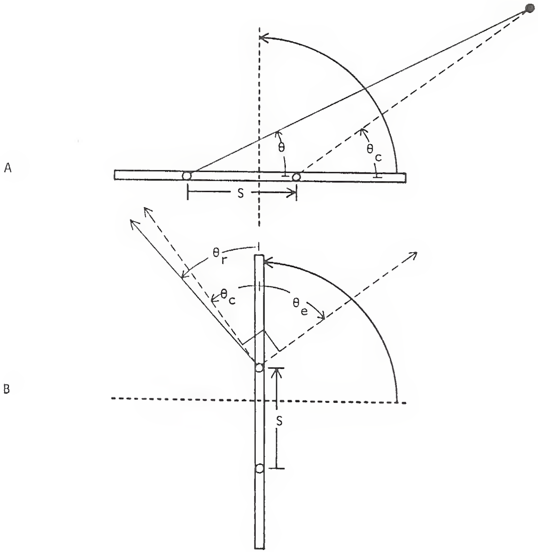


Figure 39. The horizontal bar before (A) and after (B) a $+90^{\circ}$ rotation in the horizontal plane, as viewed from above. Rotation takes place during the pursuit run of magnitude S. In (B), dashed vectors indicate two possible directions of reorientation. θ_e is an angle of reorientation (measured with reference to the bar) which is predicted by the spider's use of fixed, external cues to determine the direction of prey. Consistent with earlier definition, θ_c is the angle of reorientation which would be expected if the spider utilized its direction of movement upon the horizontal bar as a reference direction to determine the direction of prey. The outer cylinder of this apparatus (0 in Figures 29 and 30) is removed for this rotation experiment; thus visual patterns within the open room are available for reference as an alternative to the use of the horizontal bar, which is rotated. Nonetheless measured reorientation angles with reference to the route (θ_r) approximate θ_c rather than θ_e, as shown in (B) above, in support of the general hypothesis that the direction of movement upon the immediate route provides the reference direction in this situation. Data is presented in Figures 40 and 41.

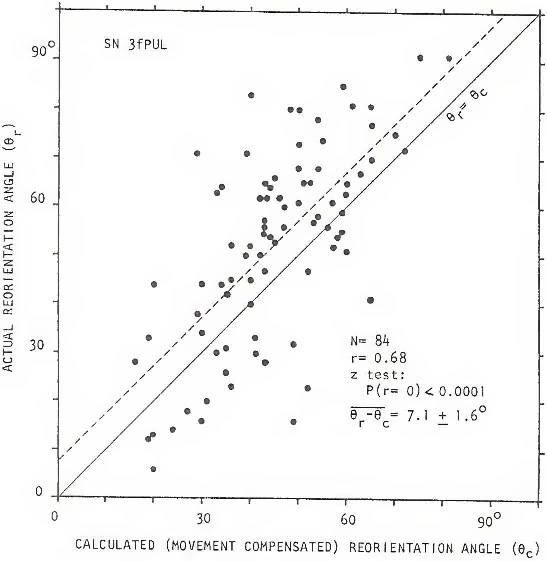


Figure 40. Reorientation by a female P. pulcherrimus after a 90° rotation of the horizontal bar during pursuit, as described in Figure 39. In every trial the spider directed its reorientation toward the same side (right or left) of the bar as its initial orientation to the prey. Regardless of the rotation of the bar in an open room, θ_c remains a highly significant, and accurate, predictor of θ_r. As shown in Figure 39, an alternative direction of reorientation based upon the use of a fixed reference system (θ_e) deviates from the direction specified by θ_c by 90°; use of the fixed reference system in this situation would lead the spider to reorient toward the opposite side of the bar from the direction of the initial orientation. This has not been observed. As for the data presented in Figure 41, roughly half of the trials presented above correspond to the "left-handed" problem shown in Figure 39; the remaining trials represent the results of the similar right-handed problem involving presentation of the prey to the right of the direction of pursuit and a rotation of -90° during pursuit.

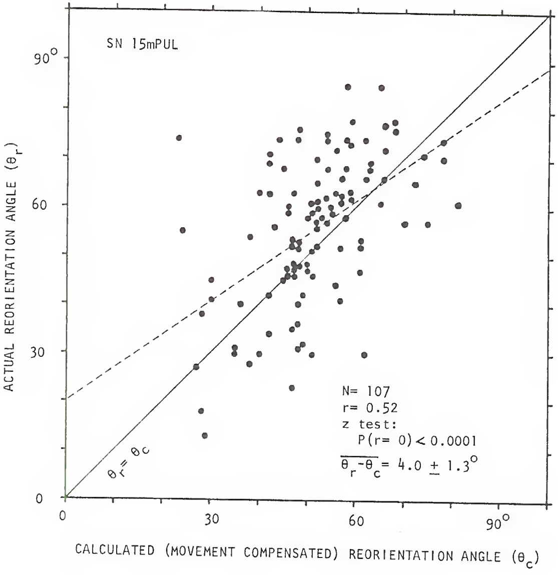


Figure 41. Reorientation by a male P. pulcherrimus after a 90° rotation of the horizontal bar during pursuit, as described in Figure 39. As for the data shown in Figure 40, every reorientation turn was directed toward the same side (right or left) of the bar as the initial orientation to prey; θ_c is a highly significant predictor of θ_r

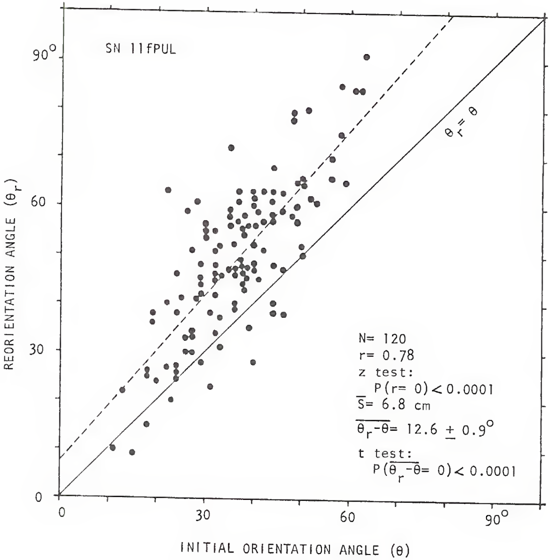


Figure 42. Reorientation turns executed on the horizontal bar in complete darkness by a female P. pulcherrimus: θ_r as a function of θ. Using the apparatus described in Figures 29 and 30, the overhead light was switched off as soon as the spider turned to run in pursuit. Only those trials in which the reorientation turn had been executed completely prior to the time at which the light was subsequently turned on (several seconds later) are shown above. In many trials, this spider did not reorient until the light was switched on, and these trials were not recorded. In one of the trials shown above, the spider was even preparing to jump in an appropriate (prey) direction as the light went on. In all respects these data compare with those collected under conditions of continuous illumination. Completion of this experiment was facilitated by the tendency of this individual to make rather long runs ($\overline{S}$= 6.8 cm) prior to reorientation.

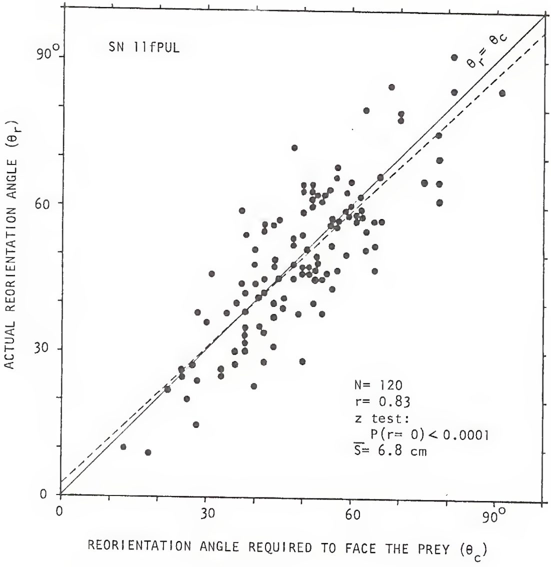


Figure 43. Reorientation turns executed on the horizontal bar in complete darkness by a female P. pulcherrimus: θ_r as a function of θ_c. Even when the reorientation turn is executed in the dark, θ_c is an accurate predictor of its magnitude. The trials shown above correspond to those presented in Figure 42.

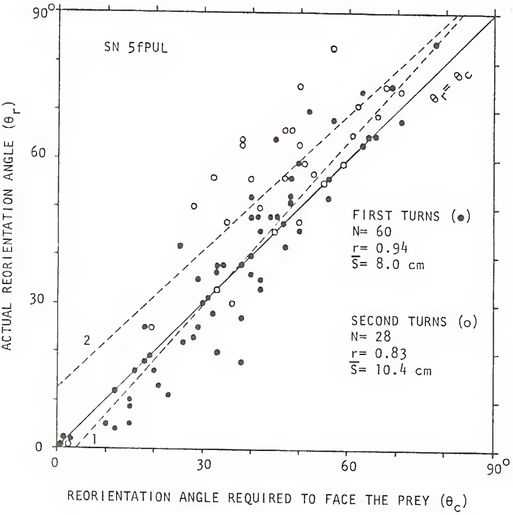


Figure 44. First and second reorientation turns executed by a female P. pulcherrimus in response to a single stimulus (for each trial). The accuracy of a second reorientation turn compares favorably with that of the first reorientation. For both turns, $P(r= 0) < 0.0001$. Numbers (1) and (2) demarcate the linear regressions (dashed lines) corresponding to the first and second turns, respectively.

Clearly, then, the angle between the initial orientation to prey and the direction of movement (θ) is a significant determinant of the reorientation angle with reference to the direction of movement (θ_r). In addition, θ is a significant determinant of S, the distance of the pursuit prior to reorientation (Figures 45-47). With reference to the definitions of θ_c, S, and L provided in Figure 28 (C), the following relationship exists:

$$\frac{d\theta_c}{dS} = \frac{\sin^2 \theta_c}{L}$$

Since sin θ_c increases to 1.0 as θ_c approaches 90°, one can conclude that the instantaneous rate of change of the angle between the route and the direction of the prey, with respect to the distance moved by the spider during pursuit ($d\theta_c/dS$) also increases as θ_c (the angle between the route and the direction of prey) approaches 90°, given a fixed value of L (distance between the prey and the route). As shown in Figure 45, the hypothesis that a fixed value of (θ_c-θ), or $\Delta\theta_c$, determines the length of pursuit prior to reorientation (S) is consistent with the central tendency of the observed behavior (allowing for considerable variation around this central tendency). A rationale for this observed tendency can be developed as follows: When θ_c is small, an accurate reorientation is possible after a longer pursuit (distance S), since θ_c is changing so slowly with respect to S. For a given prey distance (D), a longer run is also required to bring the spider to the closest approach possible on a particular linear route, when θ_c (initially equal to θ) is small. Conversely, when θ_c is larger (approaches 90°), more compensation for movement relative to the prey is required in the determination of a reorientation direction, due to

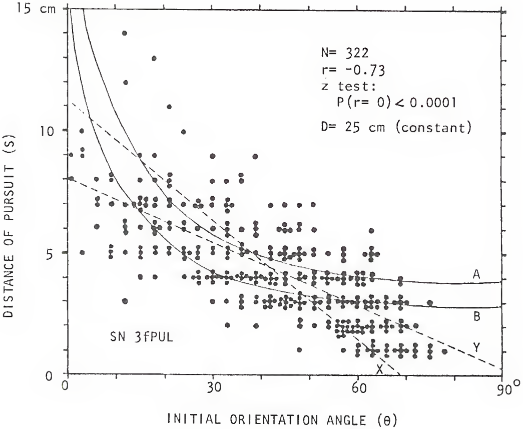


Figure 45. Behavior of a female P. pulcherrimus on the horizontal bar: S as a function of θ. Data from this set of trials are also shown in Figures 31 and 32. This spider exhibits a highly significant tendency to run a greater distance when the prey appears at a smaller angle with reference to the direction of movement. Both linear regressions of S on θ (Y) and θ on S (X) are shown above as dashed lines. Curves (A) and (B) are based upon the equation [$S = H(\cos\theta - \sin\theta/\tan\theta_c)$], where $\theta_c = (\theta + 11^\circ)$ and H is equal to either 20 cm (curve A), or 15 cm (curve B). If the position at which the spider stops to reorient were determined by a change in the respective direction of the prey (indicated by θ_c with reference to the direction of movement) of a fixed magnitude (in this case 11°, corresponding to a central tendency shown in Figure 31), then, depending upon actual H values ("distance estimates" as defined in Figure 28 (C); values used to define the curves above are consistent with data presented in Figures 55-57), curves such as (A) and (B) above could be expected to describe the relationship of S and θ with some accuracy. Although, as indicated above, θ is a highly significant determinant of S, the latter also varies greatly for any given value of θ.

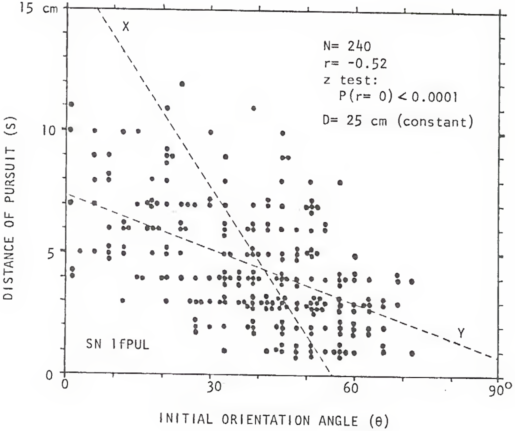


Figure 46. Behavior of a female P. pulcherrimus on the horizontal bar: S as a function of θ. As in Figure 45, both linear regressions are shown. Although θ is not as precise a determinant of S for this individual, a highly significant negative correlation does exist between the two values.

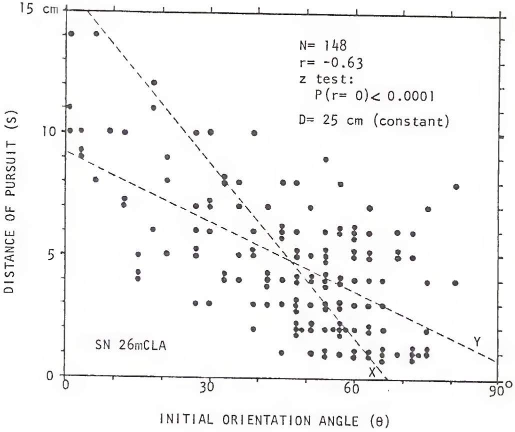


Figure 47. Behavior of a male P. clarus on the horizontal bar: S as a function of θ. Both linear regressions are indicated as dashed lines.

a higher rate of change of θ_c with respect to S when the former is large (near 90^o). A decision to either jump or change to a new secondary objective is more imminent when the spider is nearer to the closest approach to prey on a particular linear route (where $\theta_c = 90^o$). Regardless of which rationale for the adaptive value (function) of this behavior is appropriate, it is clear that θ can play a significant role in the determination of S. As θ increases, the observed value of S tends to decrease (Figures 45-47); nonetheless it is equally clear that, given a particular value of θ, S varies greatly.

The determination of an accurate reorientation angle (a value of θ_r which approximates the calculated θ_c) involves more than an ability of the spider to employ a memory of θ, as shown above. Based upon definitions provided in Figure 28 (C), one can conclude that θ_c is a function of D (the initial distance of the prey), θ (the initial direction of the prey with reference to the route of access), and S (the distance of movement along that route prior to reorientation):

$$\theta_c = \tan^{-1} \left[\frac{\sin \theta}{\cos \theta - (S/D)} \right]$$

By this analysis, the spider should be able to integrate these 3 forms of information (D, θ, and S) in developing an accurate appraisal of the relative direction of the prey with reference to the route (θ_r).

It is possible that the fact that θ_r is significantly greater than θ could represent the use of a simple adaptive output by the spider, based upon an ability to remember θ combined with the neurological analog to the generalization that θ_c is always greater than θ to some extent. This might in itself provide a reorientation angle of sufficient accuracy in most cases, independent of an ability to evaluate S.

For this reason, the modified horizontal bar described in Figures 48 and 49 was employed to measure the role of S as a determinant of θ_r when θ is a constant (35^o). As shown graphically in Figures 50-54, a highly significant positive correlation between S and θ_r, as predicted by the equation given above, does in fact exist. In this experiment, variation in S is an intrinsic feature of the behavior of each individual *Phidippus*, when presented repeatedly with the same problem of access.

It appears, then, that *Phidippus* can utilize a memory of the extent of their own movement (S) during pursuit to determine an appropriate θ_r. Previously, the ability to retain a functional memory of distance travelled has been demonstrated for certain Hymenoptera (*Apis mellifera*: Frisch and Jander, 1957; Gould, 1975; *Cataglyphis bicolor*: Burkhalter, 1972; Duelli, 1976). Apparently certain spiders, including the agelenid *Agelena labyrinthica* (Dornfeldt, 1975b) and the ctenid *Cupiennius salei* (Barth, 1976) similarly retain information with reference to the distance travelled (translation) during a relatively short foray in pursuit of prey. It is possible that the dragline is employed by these spiders in the measurement of route length, although this is not known for certain. Subsequent to a presumed evaluation of prey distance by *Phidippus*, a fixed length of silk line is played out during the predatory jump (see Figure 61, below). In this case, at least, the amount of silk played out should correspond to an estimate of the prey distance. A *Phidippus* may, conversely, be able to determine the extent of its own movement by monitoring the quantity of silk which is played out during that movement. Other methods, including the

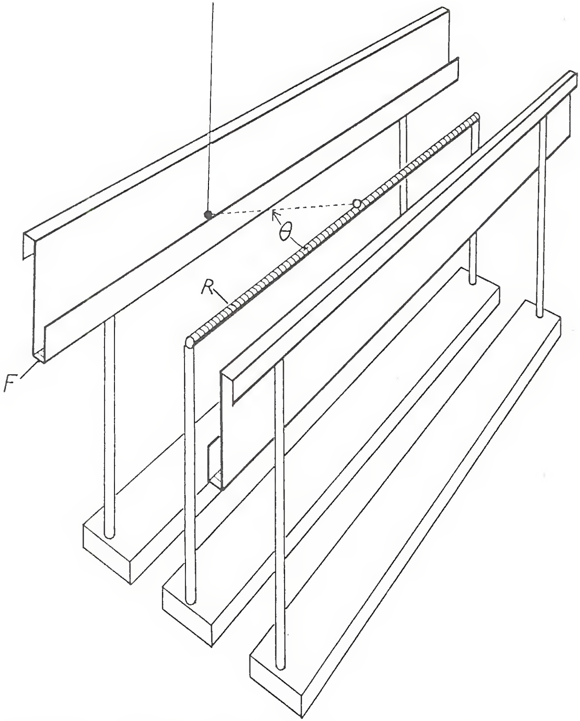


Figure 48. Perspective drawing of horizontal bar in corridor. Spider positions are read from the (R) scale on the bar, and orientations in the horizontal plane are read from an (F) scale, as shown above. The horizontal bar is 70 cm long; each of the walls of the corridor consists of a 100 cm long screen of heavy white paper. See also Figure 49.

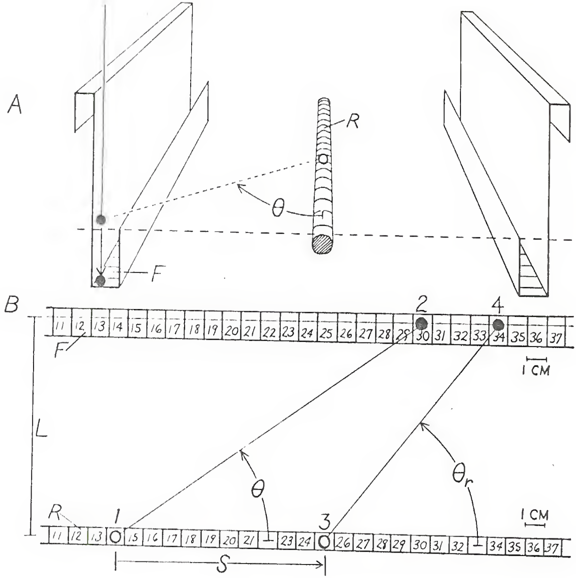


Figure 49. Perspective view (A) and horizontal plane projection (B) of horizontal bar in corridor (also shown in Figure 48). A: After the spider (open circle on scale R) sights prey (solid circle at left) at an angle θ (measured in the horizontal plane), the prey can be dropped into a trough as shown at left, and thereby concealed from the spider during the pursuit and subsequent reorientation. B: The value of θ, S, and θ_r are determined from recorded values 1-4, taken from the R and F scales respectively, as shown above. By presenting the prey to the spider at a constant position relative to the spider position in each trial, θ can be held constant (near 35°), regardless of the position of the spider. Given this fixed value of θ, the prey distance (D) is varied by placing the screen (F scale, above) at different distances (L) from the horizontal bar (R scale).

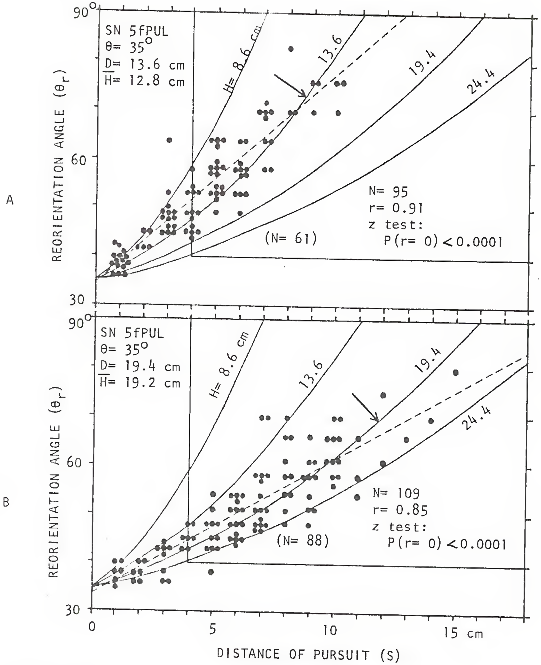


Figure 50. Behavior of a female P. pulcherrimus on the horizontal bar in response to a constant θ (35°), for prey distance (D)= 13.6 cm (A), and D= 19.4 cm (B): θ_r as a function of S. Four reference curves are defined by the function $[\theta_r = \tan^{-1}(\sin\theta/\cos\theta - S/H)]$ for each graph, based upon values of H (cm) which are given beside each of the curves. In this, and subsequent figures, an arrow is used to demarcate the curve which corresponds with an accurate determination of D by the spider (as predicted by θ_c; for points on this line $\theta_r = \theta_c$ and H= D). For subsequent comparison (Figures 55-57), H values are calculated for runs of at least 4 cm, and θ_r of at least 40°, as delimited in each graph by the inset rectangles. H determinations from shorter runs are considered to have less accuracy. Values of N given in parentheses pertain to the number of trials which are thereby employed in the determination of $\overline{H}$.

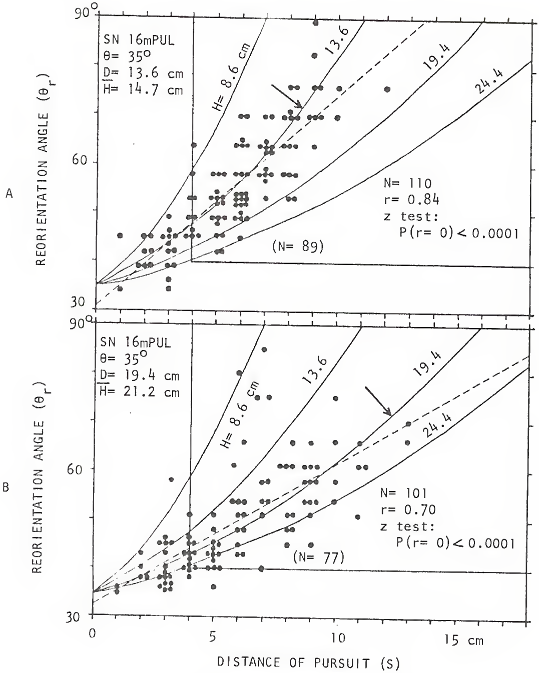


Figure 51. Behavior of a male P. pulcherrimus on the horizontal bar in response to a constant θ (35°), for D= 13.6 cm (A) and D= 19.4 cm (B): θ_r as a function of S. See Figure 50 for interpretation.

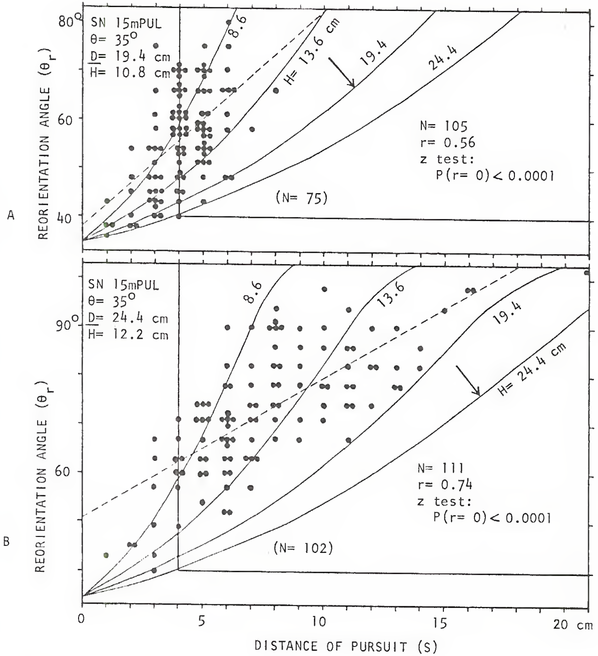


Figure 52. Behavior of a male P. pulcherrimus on the horizontal bar in response to a constant θ (35°), for D= 19.4 cm (A) and D= 24.4 cm (B): θ_r as a function of S. For interpretation see Figure 50. Although the correlation of S and θ_r is highly significant for this individual, H values are significant underestimates of D in each case.

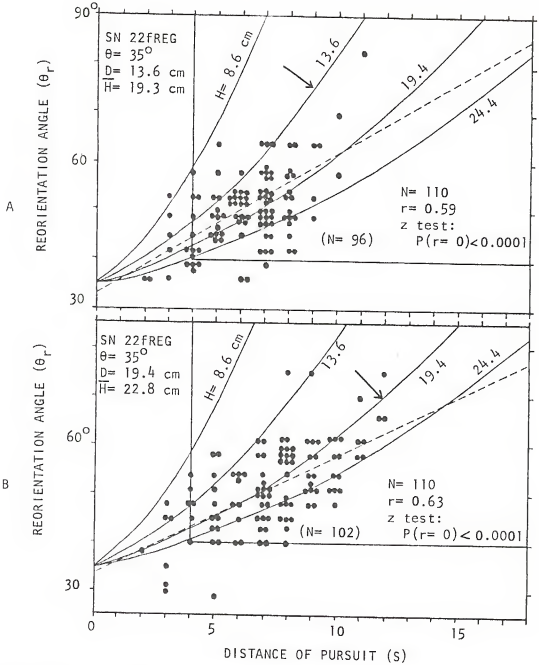


Figure 53. Behavior of a female P. regius on the horizontal bar in response to a constant θ (35°), for D= 13.6 cm (A) and D= 19.4 cm (B): θ_r as a function of S. Interpretation of curves and treatment of H determinations is consistent with Figure 50.

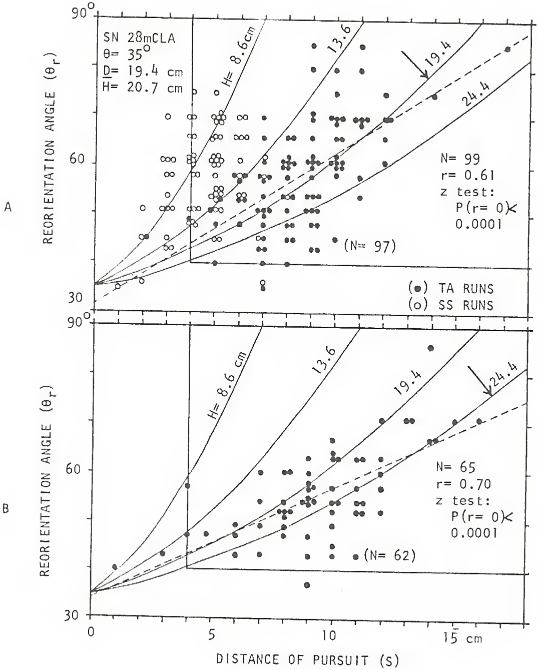


Figure 54. Behavior of a male *P. clarus* on the horizontal bar in response to a fixed θ (35°), for D= 19.4 cm (A) and D= 24.4 cm (B): θ_r as a function of S. Interpretation of curves follows Figure 50. At D= 24.4 cm, every run followed a turn away (TA) from the prey. For D= 19.4 cm, however, a significant number of the runs involved side-stepping (SS), as the spider maintained visual contact with the screen during pursuit. For D= 14.6 cm (data not shown), virtually all of the pursuits of this spider involved side-stepping. The statistical analysis in (A), above is concerned only with the TA runs. For the SS runs at this distance, N= 76, r= 0.32, P(r= 0)< 0.005, H= 10.7, and N= 58 runs were used in the subsequent analysis of H (Figure 56). H values for SS runs are much smaller than the actual value of D.

counting of steps during movement, would also suffice to provide distance (S) information for the salticid.

As shown in Figures 50-54, each collection of correlated values of S and θ_r can be approximated (central tendency) by a function based upon a fixed value for the "estimate" of prey distance, or H, as it is defined in Figure 28 (C). By definition:

$$H = \frac{S}{\cos\theta - (\sin\theta/\tan\theta_r)}$$

This corresponds to the relationship of D to θ_c:

$$D = \frac{S}{\cos\theta - (\sin\theta/\tan\theta_c)}$$

Since each trial produces measurements of S, θ, and θ_r, it is possible, by definition, to calculate a value of H for each trial. As defined in Figure 28 (C), it is convenient to refer to H as an estimate of D (prey distance) by the spider, an estimate which is implicit in the segment of pursuit which is measured. In combination with θ and S, H (as an estimate of D) would provide the final piece of information necessary for the determination of θ_r:

$$\theta_r = \tan^{-1}\left[\frac{\sin\theta}{\cos\theta - (S/H)}\right]$$

This agrees with the relationship of θ_c to D, as it is described above.

Consistent with this analysis, the data presented in Figures 50-54, as evaluated in Figures 55-57, show that a change of D (prey distance) can have a significant effect upon $\overline{H}$. The accuracy of $\overline{H}$ as an estimate of D varies considerably from individual to individual; certain individuals exhibit a remarkable accuracy in this regard (Figures 55, 56) within a certain range. The upper limit for accurate

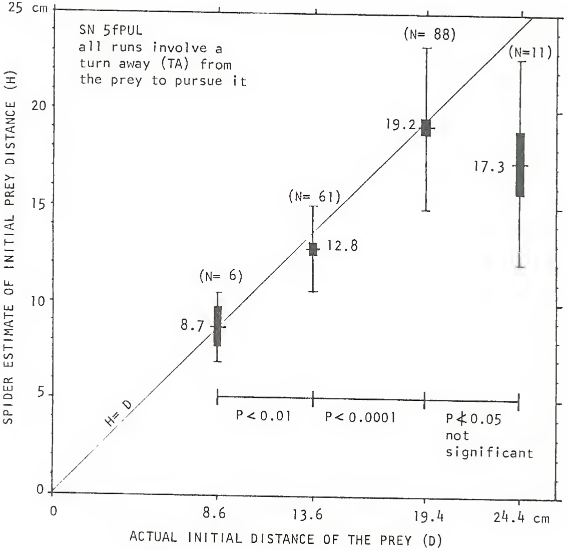


Figure 55. Comparison of H and D values for pursuits of a female P. pulcherrimus on the horizontal bar at a constant θ. Some of these data are also presented in Figure 50. For each value of D, the mean value of H is given. The thick vertical bars correspond to ± 1 standard error of this mean H, while the vertical lines indicate ± 1 standard deviation of the range of calculated H values. P values, below, indicate whether or not the difference between the respective means is significant (probability of null hypothesis based upon the use of Student's t test). At D= 8.6 cm, 47/53 pursuits involved side-stepping (SS) rather than turn-away (TA) pursuit; the former are not included in this analysis. One can conclude that D has a significant effect upon the measured value of H.

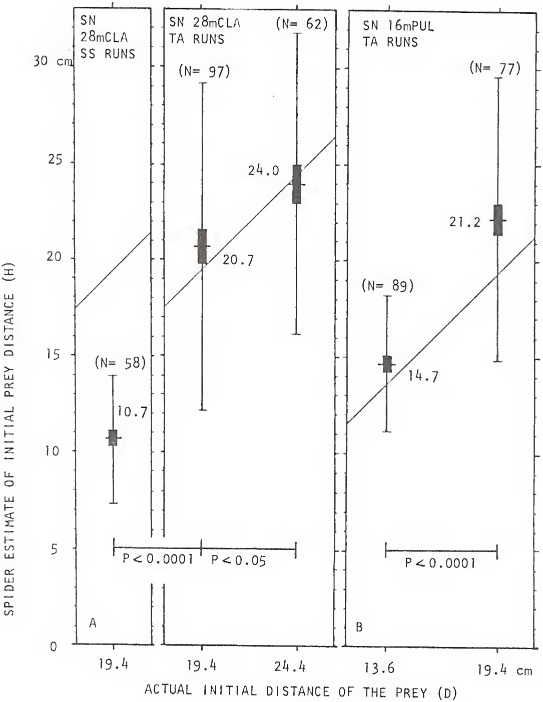


Figure 56. Comparison of H with D, for pursuits on a horizontal bar. The format is described in Figure 55. A: (see also Figure 54) The SS (side-stepping) pursuits of this male P. clarus involve a significantly lower value of $\bar{H}$ (intrinsic distance estimate corresponding to a small turning radius during pursuit) than do the TA (turn away) pursuits of this individual in response to prey at the same distance (19.4 cm). The latter [described below in Figure 60 (D)] are quite accurate, by comparison. B: (see also Figure 51) A change in the distance of prey presentation (D) has a significant effect upon the behavior of this spider; the range of distance resolution for this individual (in this situation) may extend, with appreciable accuracy, to about 20 cm.

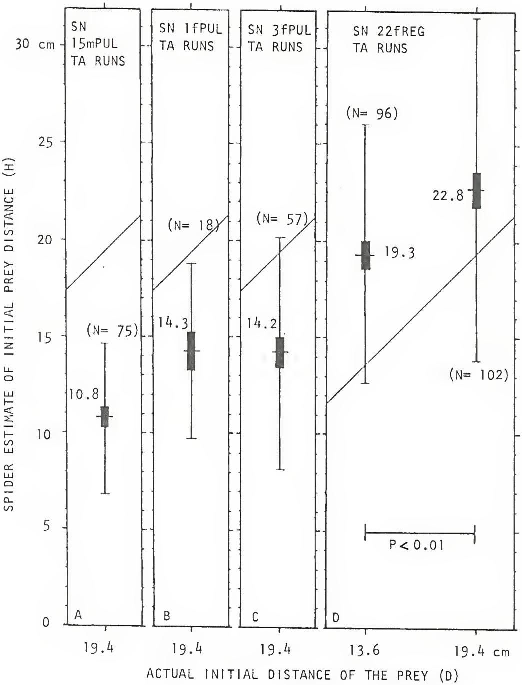


Figure 57. Comparison of H with D, for pursuits on the horizontal bar. The P. pulcherrimus for which data are presented here (A-C) consistently underestimate the distance of prey at 19.4 cm by a significant margin: the limit of distance resolution by these spiders for this particular prey stimulus (standard lure) and apparatus is assuredly less than 20 cm. The female P. regius (D) consistently overestimates as shown above: the extensive range of variation in H values for this spider (see Figure 53) suggests that it is having some difficulty with the accurate resolution of the distance of the prey in this situation. The format is described in Figure 55.

resolution of prey distance (D as a predictor of the observed H) in this particular experiment may range from 10 to 20 cm for different P. pulcherrimus. In general this is consistent with the earlier analysis of the limits of binocular depth discrimination for small objects by these spiders. In more natural situations the presence of larger plant configurations associated with the position of the prey could provide sufficient information for the resolution of much greater distances. This is a subject which clearly deserves further study.

The distance estimate (H) is not a direct measurement of the resolution of prey distance (D) by Phidippus. Implicit in the definition of H is the generalization that the spider can evaluate, and integrate, the other determinants of θ_r (which are θ and S) with complete accuracy; this is surely not the case. In a sense, then, all of the error in the execution of the reorientation turn is accumulated in the H value, as it is defined. In this regard, H is better viewed as an indicator of the accuracy of the entire segment of pursuit, encompassing the collection and integration of D, θ, and S information, as well as the accuracy of execution of the reorientation turn itself. Thus H may be viewed as an indicator of the lower limit for the resolution of prey distance by the spider.

The H values determined for side-stepping pursuits [Figures 54 (A) and 56 (A)] are significantly lower than the actual distance of the prey, for pursuits upon the horizontal bar. Since the side-stepping approach is most frequently utilized when the spider is relatively close to the prey, it is unlikely that these low H values result from a lack of ability to resolve distance. The increased rate of turning (or $d\theta_r/dS$) which corresponds with this lower value of H for the side-stepping pursuit may be a specific response to the loss of visual (AME and ALE) contact with the prey. In a functional sense this behavior may be related to the use of small survey turns in place by the salticid, as if it were attempting to find something in particular. Side-stepping does, in fact, represent an attempt by the spider to retain its direct orientation to the prey during pursuit. To do this, the spider can ordinarily rely upon continuous visual feedback from the sighted prey, as long as that prey remains in position. In contrast, the spider does not rely upon this visual information during the course of a pursuit which is initiated by a turn (of magnitude θ) away from the prey to follow a route directly. The two alternative behaviors (involving either continuous, or interrupted orientation to the primary objective during pursuit) represent two distinctly different strategies of approach to sighted prey.

Additional evidence for the ability of Phidippus to evaluate both θ and D lies in the determinative effect of these variables upon the initiation of pursuit (Figure 58).

In certain circumstances (Figure 59), θ_c and the observed θ_r can exceed 90^o. Although the horizontal bar experiments described here utilize values of θ which vary between 0 and 90^o, qualitative observation of many other problems of pursuit suggests that there is no limitation on the direction of the immediate route with reference to the prey direction, and θ_c (or θ_r) may vary freely between 0 and 180^o. Movement toward positions where a large θ_r is required is dependent upon the setting of a secondary objective to determine the direction of movement upon the immediate route, as noted in the previous section.

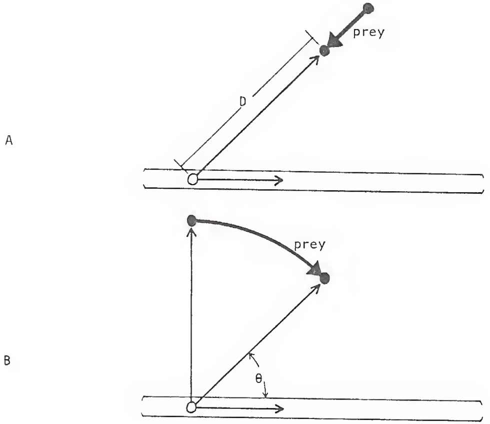


Figure 58. Prey distance (D) and direction relative to the route of access (θ) as determinants of pursuit. A: As prey is moved toward the waiting spider (open circle), a critical distance (D) is attained, at which the spider will turn to run along the bar in pursuit. In this demonstration, θ remains constant as the prey (lure) is moved toward the spider. B: θ decreases as a constant D is maintained. A critical value of θ (maximum) is attained, as shown, at which the spider will turn away to run in pursuit. Specific values of D and θ in these demonstrations vary with the selected value of the fixed θ in (A), and the value of D in (B). They also depend to a great extent upon the immediate experience of the individual, or the disposition of the individual. Nonetheless, these simple demonstrations suggest the ability of Phidippus to evaluate both D and θ from a waiting position, as determinants of subsequent behavior.

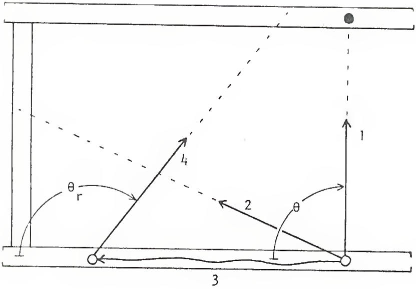


Figure 59. The reorientation angle (θ_r, as an approximation of θ_c) can exceed 90°. Here the spider orients to the prey (1), turns to face a secondary objective (2), runs in pursuit of the secondary objective (3), and reorients (4) with a turn which exceeds 90°.

It has already been shown (Figures 42 and 43) that the execution of an accurate reorientation turn (θ_r near θ_c) does not require any visual feedback. Although the spider may, under normal circumstances, orient visually with reference to its route, such visual information is not required for an accurate reorientation to prey during pursuit. An imperative question, then, is the explicit nature of the mechanism of orientation with reference to the direction of movement upon an route (θ orientation).

Mittelstaedt-Burger (1972) proposed a classification of oriented behavior into its respective *allothetic* (based on external, or environmental information) and *idiothetic* (based on internal information, either by efferent copy of directives or by the reafference provided by proprioceptors) components. Earlier, Jander (1970) set forth a similar distinction between the orientation and coordination components of patterned movement. In essence, this distinction depends upon the ability to discern whether the *information* utilized to determine a direction is internal or external in origin.

When *Phidippus* is running a pursuit on a horizontal bar, physical contact with the bar can provide a continuous source of *allothetic* information pertaining to the orientation of the bar itself. As noted above, vision could also contribute to the allothetic orientation of the spider with reference to the route, but the ability of these spiders to run with great speed and coordination along such a route in virtually complete darkness shows clearly, once again, that visual information is not required for orientation to the route.

Both *Agelena labyrinthica* (Agelenidae; Holzapfel, 1933; Görner, 1958; Moller, 1970) and *Zygiella x-notata* (Araneidae; LeGuelte, 1969) can execute 180° turns without the use of an external reference direction. Directed turns of this sort are subject primarily to idiothetic, or coordination, control. Demonstrations of idiothetic control are based upon the ability of these animals to maintain at least a short-term memory of a particular direction (for Agelena and Zygiella this is the relative direction of the retreat) with reference to the orientation of the body axes in space. As described previously, the ability of salticids to execute an accurate orientation turn to face a potential prey provides an even more dramatic demonstration of the relationship between internalized directional information and the coordinated execution of a corresponding directed turn. Presumably θ information can be acquired in a related, but inverted, manner: The execution of a directed turn (toward the route) might be the source of information of the relative direction of prey with reference to that route (θ). The possibility that θ can be determined visually also exists, however, as indicated by the role of θ in determining the probability of pursuit [Figure 58 (B)]. The combination of D, θ, and S may be considered to constitute an integrated idiothetic determinant of the reorientation angle (θ_r).

In many respects, the role of θ in particular as an idiothetic determinant of θ_r may be compared with the more general demonstration of the ability of arthropods to compensate for a forced turn in one direction with an appropriate turn in the opposite direction when allowed to do so (reverse turning), in order to maintain a course (Akre, 1964; Wilson and Hoy, 1968; Burger, 1971; Schäfer, 1975a, 1975b). Both phenomena are concerned with an ability to determine a change in direction of movement, and to remember the extent of this turn. The reverse turn itself can be compared with reorientation. Phidippus can also maintain a fairly straight course on a horizontal surface in near darkness, weaving alternately to the right and left.

Regardless of the coordination inherent in the movements of these spiders, the continuous availability of physical contact with the route itself as an allothetic reference direction must always be considered. In normal situations the route direction (allothetic reference) and the orientation of the prosoma (idiothetic reference) are generally in alignment during the pursuit, and both probably contribute to the use of the route as a reference direction, since both are part of the immediate experience of the spider. For this reason, θ orientation refers to the use of both the direction of movement (idiothetic component) and the direction of the route itself (allothetic component) as reference directions in space. Several qualitative observations of pursuit which are consistent with the use of the route as an allothetic reference direction are shown in Figure 60.

Phidippus can readily distinguish between right and left alternatives in the determination of a reorientation turn. Every reorientation turn which has been measured on the horizontal bar was directed toward the same side (either right or left) of the bar as the initial orientation turn ($P < 0.0001$). This includes every one of the reorientation turns executed in complete darkness as described in Figure 42, a demonstration which shows clearly that this "handedness" does not depend upon any form of visual reference to the surroundings.

In summary, Phidippus can integrate estimates of prey distance (D), the direction of prey relative to the direction of movement upon a route (θ), and the distance moved along that route (S) to determine an

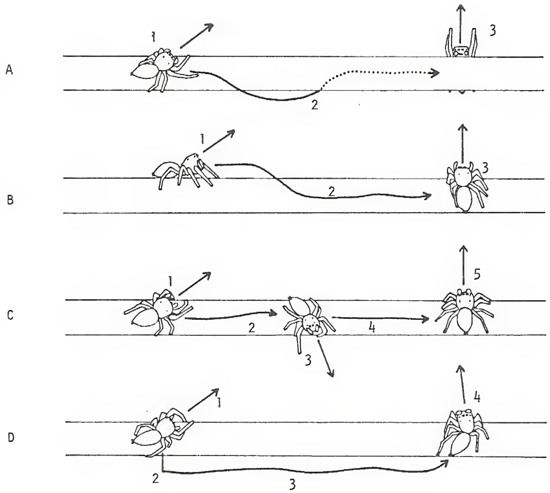


Figure 60. Phidippus is not locked into a simple reverse turn pattern as it determines the direction of reorientation. A: After initially sighting prey to the left from the top of the bar (1), the spider runs (2) and reorients in the appropriate direction by turning very quickly to the right when beneath the bar (3). B. An initial β orientation to the prey (1) is followed by an α reorientation (3), involving a completely different pattern of motor control. C: After distraction (3), the spider continues its pursuit (4), and executes a fairly accurate reorientation (5). D: Some individuals (including SN 5fPUL, 16mPUL, and 28mCLA) routinely step to the opposite side of the bar (2) from the prey direction, prior to a very steady-paced walk in pursuit (3), followed by, in general, a remarkably accurate reorientation turn (4). These are the individuals with the most accurate H (distance estimate) values, and they generally orient for a longer period of time (in position 1) prior to pursuit than do most individuals in this situation. Each of these events (A-D) has been observed many times.

accurate reorientation angle (θ_r as an approximation of θ_c) with reference to the direction of movement. This use of the immediate direction of movement upon a route of access to an objective as a reference direction (whether idiothetic or allothetic) for the specification of the direction of that objective in space is termed θ orientation.

SECTION X
ORIENTATION WITH REFERENCE TO GRAVITY (γ ORIENTATION)

For a terrestrial organism, the force of gravity is an omnipresent fact of life. As a potential reference direction for orientation, the force of gravity is totally dependable. Plant configurations may at times be ambiguous or obscured from the view of the spider, but gravity is always readily available to provide a fixed reference direction, irrespective of any other reference systems that might be employed. As a convention, directions with reference to gravity are specified by their inclination (γ), where γ is the angle between the specified direction and its projection upon a horizontal plane. Directions above the horizontal plane are assigned positive γ values; those below the horizontal plane have negative γ values. Therefore γ varies from a maximum of $+90^\circ$ (straight up) to a minimum of -90° (straight down).

There is a great deal of general evidence for the ability of the salticid spider to orient with reference to gravity. *Phidippus* virtually always run along the top of horizontal bars; the tendency of these spiders to move to the upper side of an inclined bar, even if it deviates by less than 10° from the vertical, can be readily demonstrated. Presumably a spider can move with greater ease on the upper surface of a horizontal route, where alternate attachment to and release from the substratum are not required to prevent falling. As noted earlier, ascent itself may be a generalized directive of the behavior of *Phidippus*.

An ability to orient within the gravitational field is also a requirement for the successful completion of a directed jump by a salticid. If the object of a particular jump is a potential prey at a distance which exceeds 2 cm, then the spider must generally aim above the actual prey (target) position if it is to attain that position during the course of ballistic flight (Figure 61).

As shown in Figure 62, the ballistic trajectories which can be employed by a Phidippus in a jump are defined by the interaction of the take-off velocity (a vector) with the constant acceleration of gravity. the value of 90 cm/sec used here as an estimate of the magnitude of take-off velocity is consistent with measurements of the take-off velocity of P. pulcherrimus (Figure 61). As γ_0 , or the inclination of the take-off vector with reference to the horizontal plane, declines a longer and more direct trajectory is possible.

There is much evidence to support the generalization that an evaluation of the potential of success of a particular jump, which accounts for the constraints due to gravity which are described in Figure 62, precedes the execution of that jump by Phidippus. To do this, these spiders must be able to evaluate the direction of the objective with reference to gravity (γ information), as a determinant of subsequent behavior. The ability of Phidippus to utilize both γ and D (prey distance) to determine whether a jump will be attempted toward a potential prey can be demonstrated directly (Figures 63-66); the maximum value of D for which a jump can be elicited correlates inversely with the magnitude of γ . This result is completely consistent with the jumping range (for accurate, or fairly straight jumps) of these spiders as determined by gravity (Figure 62), as well as with the

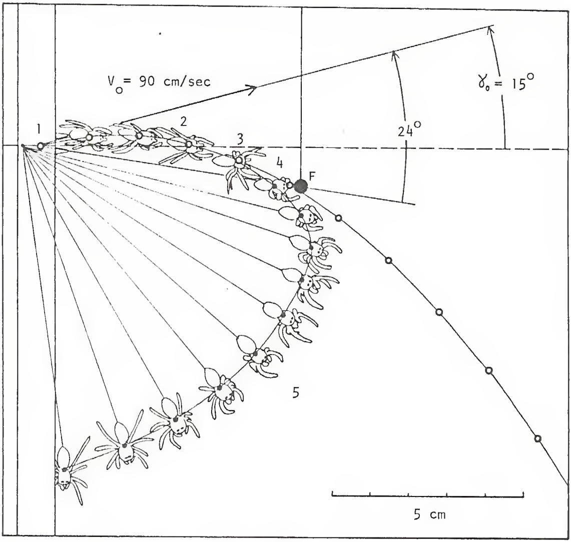


Figure 61. Predatory jump of an adult female Phidippus pulcherrimus. Sequential positions of the spider at 15 msec intervals are shown in outline above; these have been traced from a photographic record of the jump obtained with the use of an electronic strobe unit as described by Parry and Brown (1959). The spider jumps from a position on a vertical wood rod (1) in response to the standard fly stimulus (F). After an essentially ballistic flight (2), the rear legs come forward (3) in preparation for a grasp (4). The legs are extended as the spider swings back to the rod as a pendulum (5). The period of ballistic flight ends (4) as the dragline is held tight; a theoretical trajectory based upon an initial velocity (V_o) of 90 cm/sec directed 24° above the prey position, which agrees with the observed trajectory, is plotted as a series of open circles at 15 msec intervals, above. In this case the execution of a successful jump requires the spider to aim above the prey position.

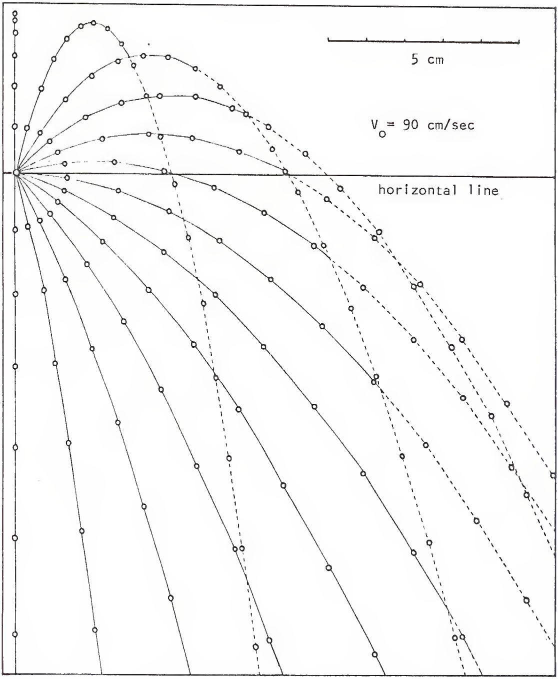


Figure 62. Potential trajectories in a vertical plane for a ballistic missle with a take-off velocity (V_o) of 90 cm/sec. Trajectories are plotted for γ_0 (orientation of take-off velocity with reference to the horizontal) values ranging from +90° (straight up) to -90° (straight down) at 15° intervals. Open circles indicate the position of the missle at 15 msec intervals. Trajectories are shown as dashed lines after the total displacement vector from the origin deviates from γ_0 by more than 30°. For smaller values of γ_0 a longer, more direct trajectory is possible.

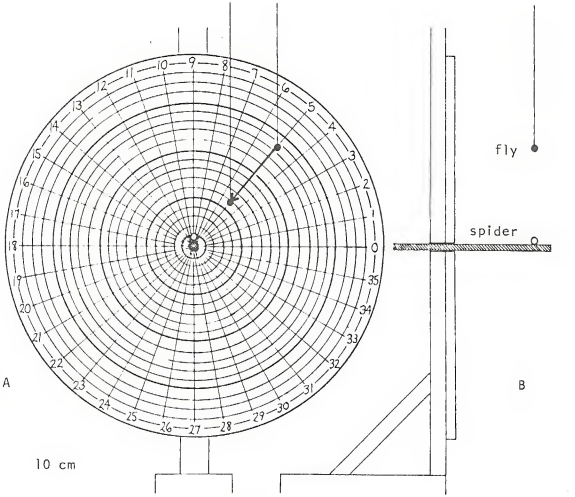


Figure 63. Front (A) and lateral (B) projections of apparatus used to map the jumping space of Phidippus in a vertical plane. In (B), the position of the spider (open circle) on a horizontal bar (shaded) relative to the fly is indicated. As shown in (A), the fly is moved toward the spider along a certain radius (corresponding to a particular value of γ, or the direction of the fly relative to the horizontal), until the spider prepares to jump. At this point, the value of D, or the distance between the axis of the bar and the prey position, is recorded. Paired (γ, D) data are presented in Figures 64-66 in a manner consistent with the view provided by (A) above. For this procedure to succeed, it is essential that the spider is highly "motivated," or deprived of food for an adequate interval in advance. The prey must also be moved slowly toward the spider, in effect testing for a response at each 0.5 cm interval along the radius.

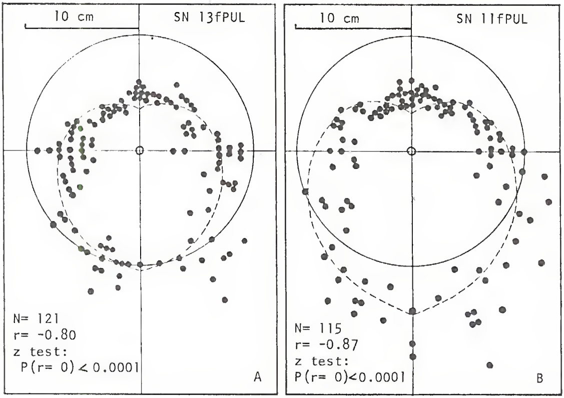


Figure 64. Jumping spaces of two female *P. pulcherrimus*, as mapped with the apparatus described in Figure 63. The dashed lined are the linear regression lines of D on γ, in polar coordinates. By definition γ (the angle between the prey direction and the horizontal reference) varies from $+90^{o}$ (straight up) to -90^{o} (straight down). Thus both linear regression and linear correlation (r) are based upon D (radial distance to prey) as a function of γ. Clearly the spiders will attempt downward (small γ) jumps at a greater distance. Here both D and γ can be considered as criteria of jumping behavior.

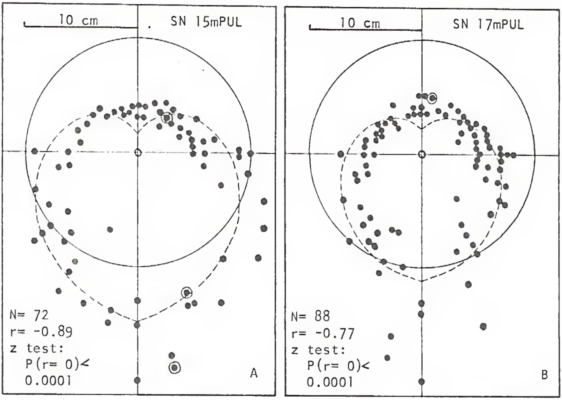


Figure 65. Jumping spaces of two male P. pulcherrimus, mapped with the apparatus shown in Figure 63. For interpretation, see Figure 64. At each of the encircled fly positions above, the spider successfully captured the fly (lure) before it could be removed.

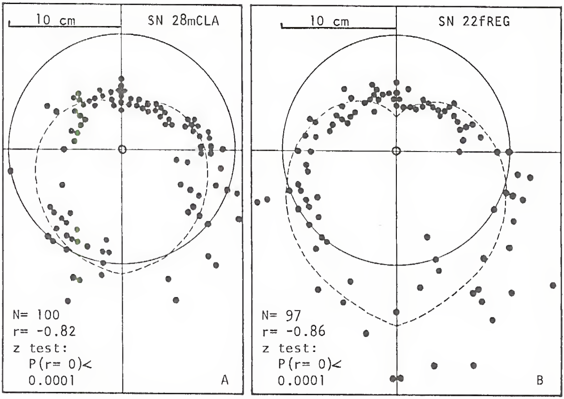


Figure 66. Jumping spaces of a male P. clarus (A) and a female P. regius (B), as mapped with the technique given in Figure 63. Interpretation is consistent with Figure 64.

general notion that these spiders will only attempt those jumps which are feasible to the extent that their information (γ, D) is accurate.

Orientation with reference to gravity also plays a highly significant role in determining the strategy of pursuit which is employed by Phidippus in a given situation. These spiders will often utilize a turn-down jump (Figure 67) during pursuit; this behavior is consistent with the fact that the range and accuracy (directness) of a jump is greater when γ is smaller. As shown in Figure 68, Phidippus will readily jump prey at a particular distance (here it is 6 cm) when γ is small (prey below); the same individuals will run a detour, if necessary, to move into a suitable position for attack when γ is large, rather than attempt a direct jump up toward the prey. Additional demonstrations of the role of γ in determining the position of attack selected by Phidippus, relative to a prey position, are provided in Figures 4 (F), 69, and 70. These demonstrations agree with the observation (Robinson and Valerio, 1977) that the tropical salticid Phiale will attack the much larger araneid Argiope in its web, by positioning above the prey position prior to launching itself upon an accurate trajectory which may exceed 12 cm in horizontal projection.

The apparatus shown in Figures 71 and 72 was used to vary the orientation of the route of pursuit with reference to the fixed gravitational field by manipulating the orientation of the running bar in a vertical plane. Whether θ (the initial angle between the prey and pursuit directions) specifies a prey direction below or above a horizontal bar (Figures 73 and 74), or to the side of a vertical bar (Figures 75-80), Phidippus can reorient accurately (observed θ_r agrees with the calculated θ_c) in a vertical plane. This result is thoroughly

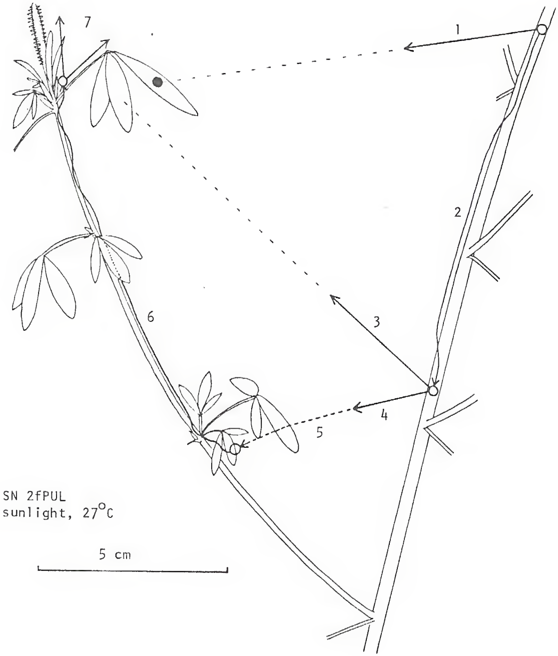


Figure 67. Use of the turn-down jump during a detoured pursuit by a female *P. pulcherrimus*. The spider orients to the prey (1), descends (2), reorients (3), turns down toward an accessible position (4), jumps (5), ascends the branch (6), and finally conducts a series of small turns (7) at the top of the branch.

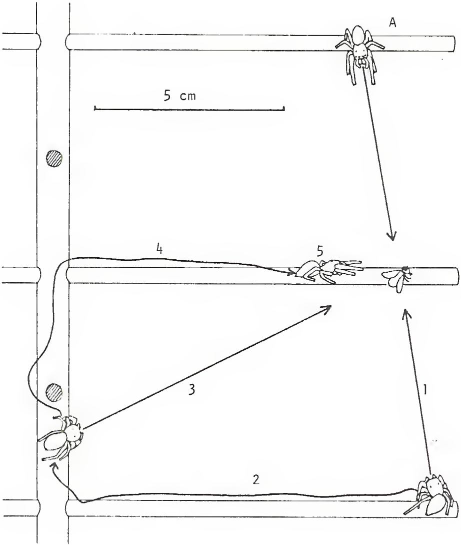


Figure 68. The influence of gravity upon the strategy of approach to sighted prey by Phidippus. A: When above the prey at this distance, the spider will attempt a direct jump. B: When below the prey at the same distance, the same spider will tend to run a detour as shown (1-5), culminating in a slow stalk (5) preparatory to the jump. Under conditions of neutral (lateral) illumination, problems A and B were presented to a female P. pulcherrimus (SN 8fPUL). Starting in position (A) relative to the prey, this individual prepared for a direct jump in 60 of 60 trials. When starting in position (B), below the prey, the same individual attempted a direct jump in only 5 of 25 trials; in 20 of these 25 trials this spider ran a detour like the one indicated above. Compared in the form of a contingency table, the behavior of this spider starting at (A) differs significantly ($P < 0.001$) from the behavior of the same spider starting at position (B) relative to the prey.

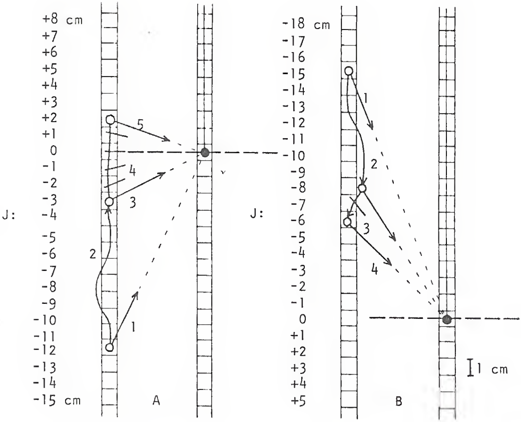


Figure 69. Selection of a jumping position relative to prey on a vertical pole. A: When approaching from above, the spider passes the closest approach to the prey (J= 0) and jumps from a position slightly above the prey position, as shown (5). B: When approaching prey from above, the spider stops to jump well above the prey position (4). Both (3-5) in (A) and (3-4) in (B) represent intervals of side-stepping, as the spider positions for a jump. For purposes of measurement (Figure 70) and comparison, the jumping position (J) is taken as either the number of cm before (-) or after (+) the closest approach to prey (where J= 0) is attained by the spider. This is indicated in the J-scale, to the left of each diagram above. Thus J= +2 cm in (A), and -6 cm in (B). For trials with P. pulcherrimus, the axes of the poles are 6 cm apart; for the larger P. regius these are 10 cm apart.

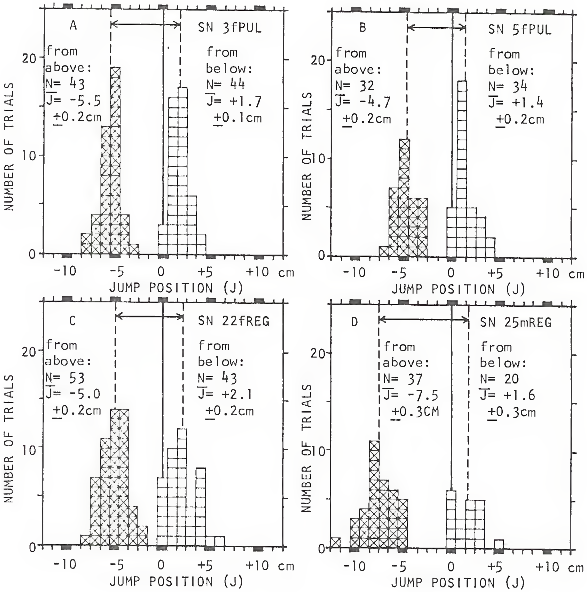


Figure 70. Frequency histograms (A-D) of J (jump position) values collected for approaches from above (crossed squares) and below (open squares) the prey, as described in Figure 69. In each case the mean value of J ± 1 standard error of that mean are given; arrows indicate the highly significant ($P < 0.0001$ for each spider) difference in the mean jumping position (J) assumed by the spider, dependent upon its approach to the prey (from above or below) with reference to gravity. Both P. pulcherrimus (A and B) and P. regius (C and D) stop short of the closest approach to prey when they approach prey at this distance from above, while they pass by the prey position to assume a jumping position above the prey when approaching from below. With either approach, then, the spider has a significant tendency to jump from a vantage position, above the prey.

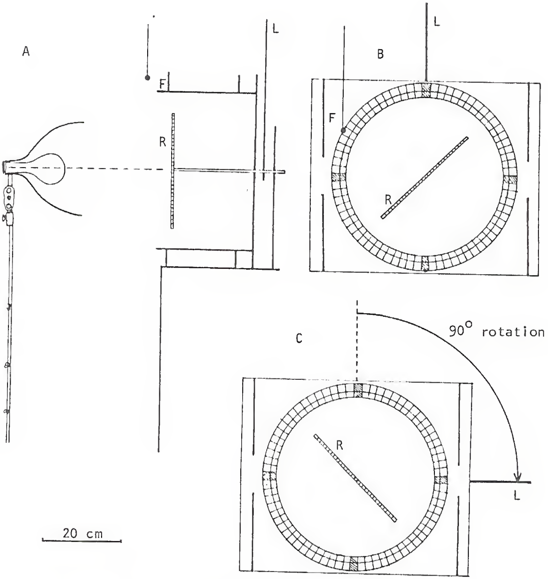


Figure 71. Vertical section (A) and frontal views (B and C) of apparatus used to measure reorientation directions in a vertical plane. Apart fron the vertical orientation, the apparatus is virtually the same as that used to measure reorientation with reference to a horizontal bar in a horizontal plane (Figures 29 and 30); measurements are made in the same manner with this apparatus. A: The lamp is in line with the central axis of the apparatus (horizontal dashed line). The observer watches the pursuit from the darkened room behind the lamp. A lever (L) allows for rotation of the bar in a vertical plane. The standard lure is shown in position (F) beside the circumferential scale. B and C: During rotation experiments, the bar is rotated 90° in a vertical plane during pursuit by movement of the lever as indicated here. The circumferential scale (F) is divided into 5° units; the running scale (R, to indicate spider positions) is divided into 1 cm units.

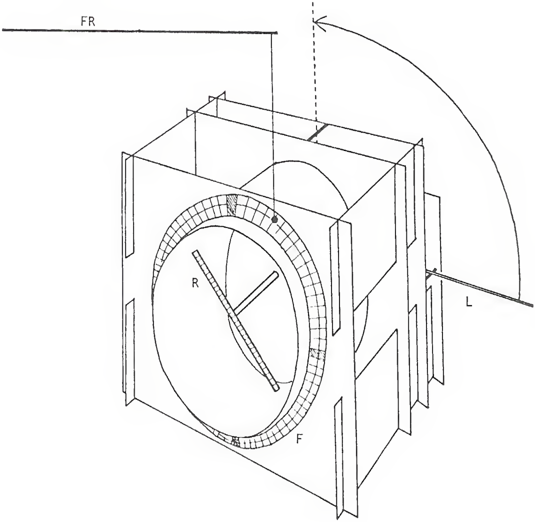


Figure 72. Perspective drawing of the apparatus described in Figure 71. The cylinder is constructed of heavy white paper, and it is supported by a cardboard framework as shown above. The running bar (R) is a 30 cm long wood dowel of 9 mm diameter; this may be rotated in a vertical plane by movement of the lever (L). The fly rod (FR) used to suspend the standard lure (dead fly at the end of a hair) is also shown above. The measurement of pursuit behavior with the R and F scales is described in Figure 30.

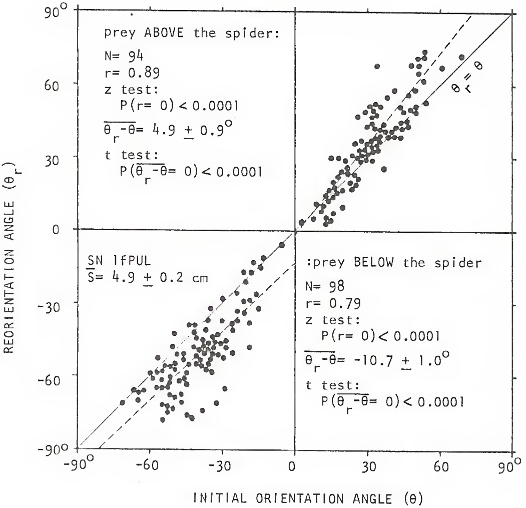


Figure 73. Reorientation in a vertical plane by a female *P. pulcherrimus* on a horizontal bar: θ_r as a function of θ_c. These data were gathered with the apparatus shown in Figures 71 and 72. As a convention, values of θ which specify a direction above the bar in the vertical plane are (+), while those which specify a direction below the bar are (-). Whether the prey appears above (upper right) or below (lower left) the horizontal bar, reorientation behavior compares in all respects with the reorientation turns executed in a horizontal plane, described earlier: The reorientation angle correlates positively with, and is significantly greater in magnitude than, the initial orientation angle.

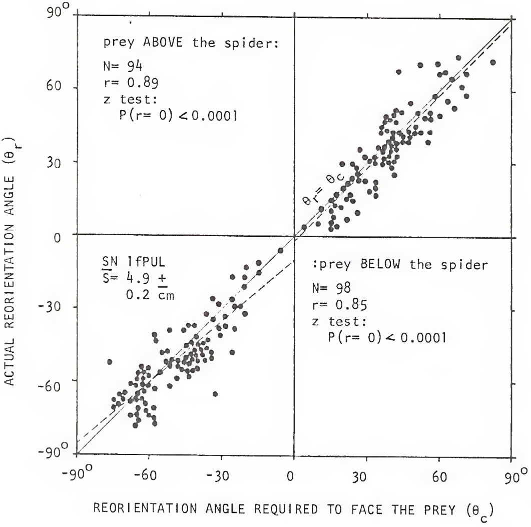


Figure 74. Reorientation in a vertical plane by a female P. pulcherrimus on a horizontal bar: θ_r as a function of θ_c. As with reorientation turns in the horizontal plane, θ_c is an effective predictor of the measured θ_r. Data from the same trials are also shown in Figure 73, where the convention for (+) and (-) values of θ determinations is also explained.

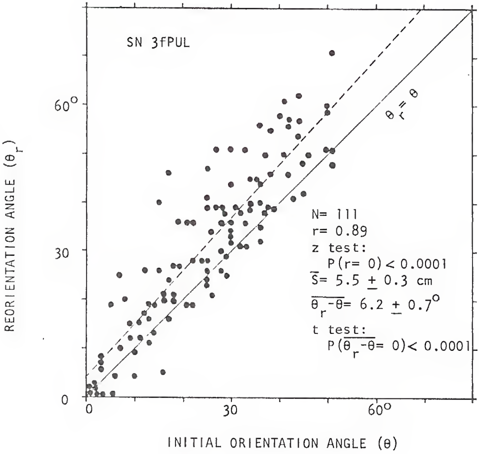


Figure 75. Reorientation behavior of a female _P. pulcherrimus_ running _down_ a vertical bar in pursuit: θ_r as a function of θ. The apparatus described in Figures 71 and 72 was used to obtain these data.

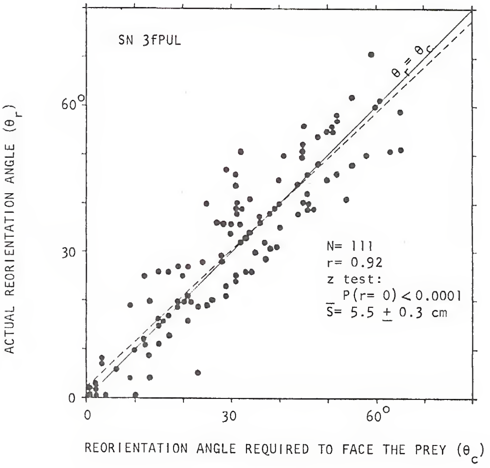


Figure 76. Reorientation in a vertical plane by a female *P. pulcherrimus* running *down* a horizontal bar in pursuit: θ_r as a function of θ_c, for trials described in Figure 75.

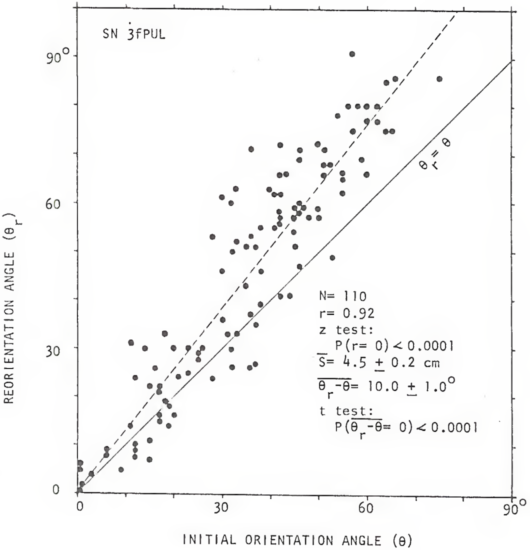


Figure 77. Reorientation in a vertical plane by a female P. pulcherrimus running up a vertical bar in pursuit: θ_r as a function of θ. The apparatus described in Figures 71 and 72 was used in the collection of these data.

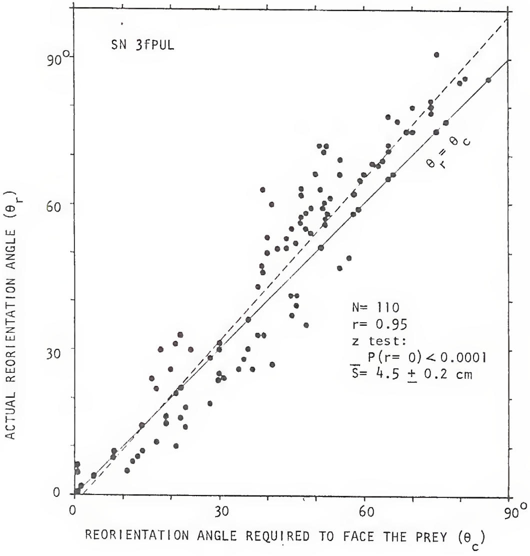


Figure 78. Reorientation turns executed in a vertical plane by a female P. pulcherrimus running up a vertical bar in pursuit: θ_r as a function of θ_c, for trials described in Figure 77.

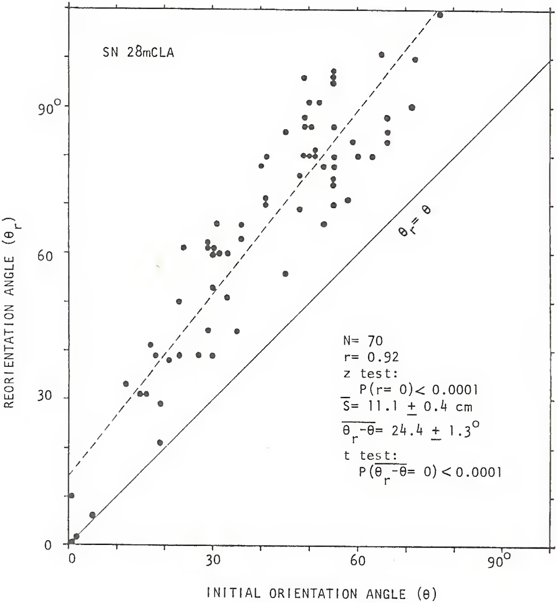


Figure 79. Reorientation turns executed in a vertical plane by a male P. clarus running up a vertical bar in pursuit: θ_r as a function of θ. This individual ran very long, fast ascending pursuits, generally on the side of the bar opposite to the prey direction.

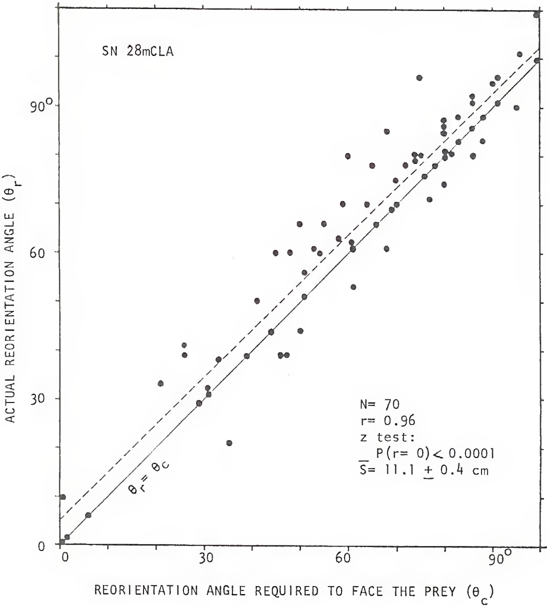


Figure 80. Reorientation in a vertical plane by a male P. clarus running up a vertical bar in pursuit: θ_r as a function of θ_c.

consistent with reorientation behavior observed in a horizontal plane. As in the horizontal plane, the spider may be using the route as a reference direction for reorientation in the vertical plane as well. Unlike the earlier problem of reorientation in the horizontal plane, however, the force of gravity is also available for reference in determining a direction in a vertical plane.

Since both γ and θ information could be used by Phidippus to determine the appropriate direction of reorientation in a vertical plane, the problem described in Figure 81, involving rotation of the bar during pursuit, was devised to place γ and θ information, which may have been acquired with the initial orientation to the prey, into conflict. The result (Figures 82-85) is that the measured direction of reorientation agrees with the use of gravity as a preferred reference system in this situation (γ_c is an effective predictor of γ_r). In a dramatic violation of all of its experience relative to the direction of the route itself (θ orientation), Phidippus will follow γ_c in determining a reorientation direction in the vertical plane. In contrast to this result, Phidippus continues to rely upon θ information when the same rotation experiment, with the addition of conspicuous and conflicting visual cues as well, is run in the horizontal plane (Figures 39-41). This rotation experiment has a counterpart in the experience of Phidippus in its natural habitat, as supporting leaves or stems may give way under the weight of the spider during a pursuit, effectively eliminating their utility as reference directions; gravity is always reliable.

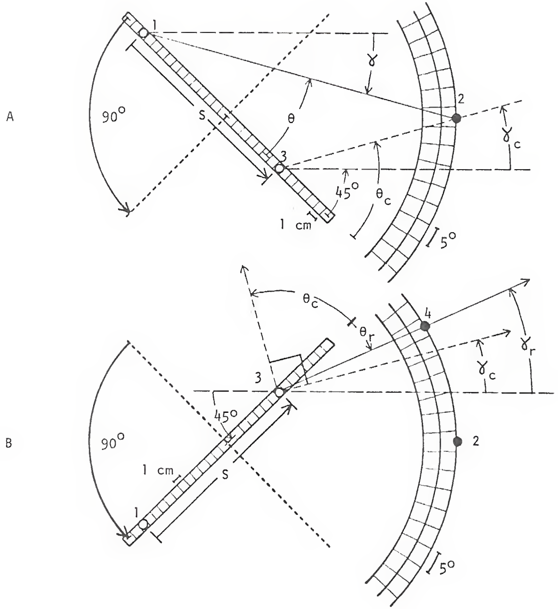


Figure 81. Running bar in vertical plane before (A) and after (B) rotation in a vertical plane during the pursuit of distance S. The apparatus is described in Figures 71 and 72. As in earlier experiments data consists of values 1-4 taken from the running bar and circumferential scales, respectively. θ_c represents the reorientation turn observed when a comparable experiment is run in the horizontal plane (Figures 39-41); this is the expected direction of reorientation with reference to the direction of pursuit. As a convention, θ values which describe directions above the bar in this vertical plane are (+); directions below the bar correspond to (-) values of θ. As shown in Figures 82-85, however, γ_c (which predicts a $\theta_r = \theta_c - 90°$) is the better predictor of the direction of reorientation (γ_r near γ_c). This can be interpreted as a demonstration of γ orientation, to the exclusion of conflicting θ information.

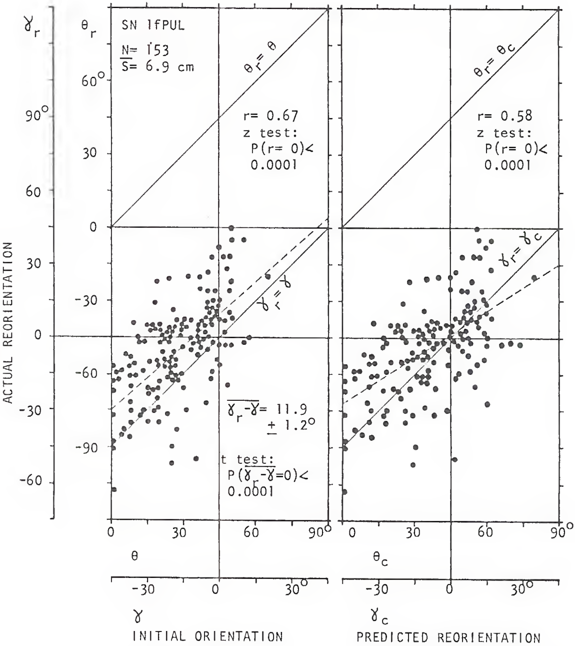


Figure 82. Results of the rotation experiment described in Figure 81 for a female *P. pulcherrimus*. Respective reorientation angles (θ_r and γ_r) are presented as a function of both the initial orientation (either θ or γ) at left, and the predicted reorientation (either θ_c or γ_c) at right. The observed values of θ_r tend to deviate by -90° from θ_c; γ_c is a far better predictor of γ_r. This distinction is particularly evident in those trials where both θ and θ_c are near 0°, but the spider reorients at θ_r near -90°, actually perpendicular to the bar despite the original sighting of the prey in line with the bar. γ_r is significantly greater than γ , an indication of compensation for movement by the spider.

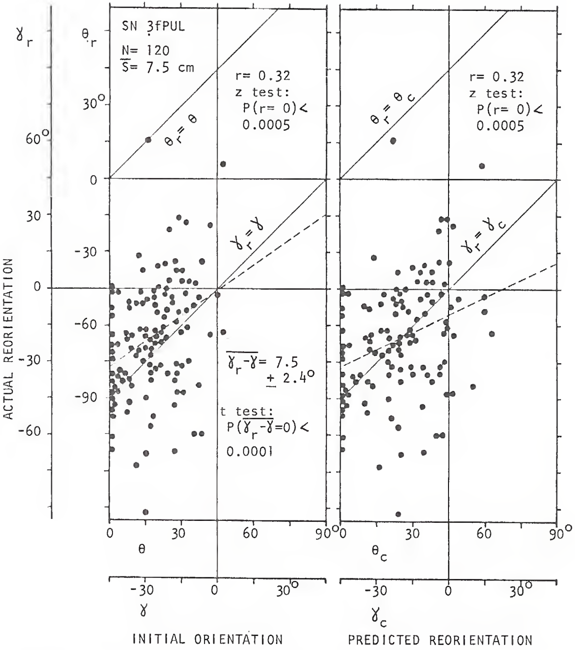


Figure 83. Results of rotation experiment for a female P. pulcherrimus. The interpretation of these data agrees with that provided in Figure 82.

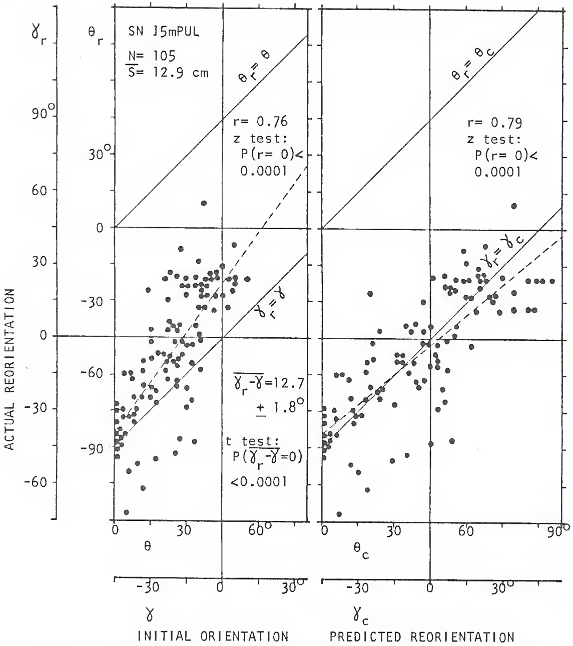


Figure 84. Results of rotation experiment for a male P. pulcherrimus, consistent with the interpretation provided in Figure 82. This particular experiment worked much better with this particular individual than with any others, due to the tendency of this spider to run each pursuit as a long, fast run ($\overline{S}$= 12.9 cm). This long pursuit allowed ample time for the smooth rotation of the bar prior to the reorientation turn. As a result, perhaps, the correlation of γ_c and the observed γ_r is particularly high for this spider.

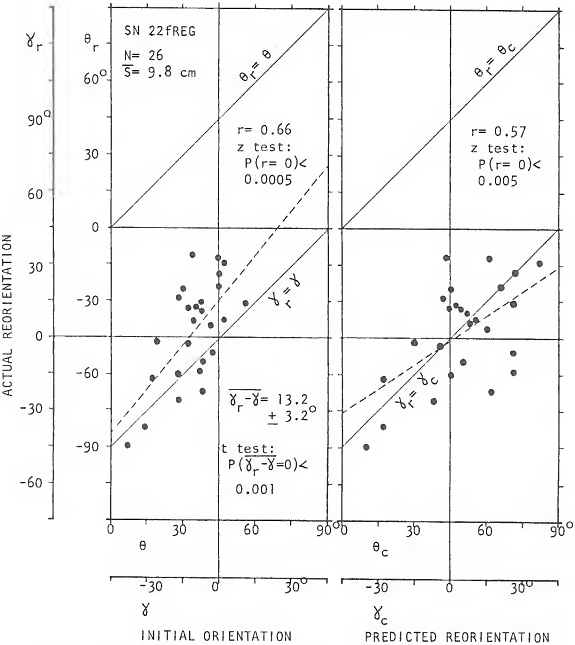


Figure 85. Results of rotation experiment for an adult female P. regius, consistent with the interpretation provided in Figure 82.

Two additional demonstrations of the generalized ability of *Phidippus* to remember a direction with reference to gravity (use γ information) are given in Figures 86-91. This ability agrees with the demonstrated ability of other spiders, including the araneids *Araneus* (Peters, 1932), *Argiope* (Robinson, 1969), and *Zygiella* (LeGuelte, 1969), to utilize the memory of a direction with reference to gravity when orienting within their webs. The agelenid *Agelena labyrinthica* can also use gravity cues, in preference to light cues, in determining the direction of return to its retreat (Bartels, 1929; Holzapfel, 1933). Many insects can also remember a direction with reference to gravity. The curious, and widespread, ability of insects to transpose the memory of a direction with reference to visual cues (light compass) into a corresponding orientation with reference to gravity is well-known (Frisch, 1949, 1967; Vowles, 1954a, 1954b; Linsenmair-Ziegler, 1970).

Specific receptors for the detection of gravity have never been demonstrated in spiders. For the most part, the *whorled setae* of spiders appear to be contact chemoreceptors, although each of these setae also contains several neurites which respond to mechanical stimulation (Foelix, 1970a, 1970b, 1976; Harris and Mill, 1973; Foelix and Chu-Wang, 1973; Drewes and Bernard, 1976; Hill, 1977a). These setae are whorled, or segmented, along their length; unlike virtually all other setae, they bend freely in response to gravity. Thus there is a good possibility that these setae, which are often numerous on the distal portion of the appendages of spiders, can provide a direct evaluation of the direction of the force of gravity for the spider.

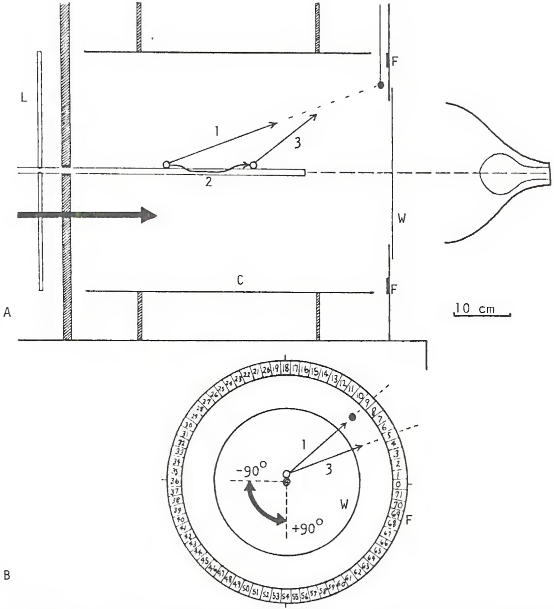


Figure 86. Vertical section (A) and observer's view (B) of apparatus used to measure the ability of Phidippus to reorient in a radial direction, using only gravity as a reference system. A: The lamp (at right) is centered behind a circular window (W) of opaque tracing paper, surrounded by a circumferential scale (F). The spider orients to the lure (1), runs in pursuit (2), and reorients (3). During each pursuit, the bar is rotated around its long (horizontal) axis with the lever (L) at left. The large arrow at left indicates the view of the observer as the spider runs toward the window, within a white paper cylinder (C). The lure is removed prior to reorientation. B: View of the spider (open circle) as seen by the observer during pursuit. The projection of orientation (1) and reorientation (3) directions onto a vertical plane is read from the circumferential scale (F) as accurately as possible. The large curved arrow indicates the extent of rotation (± 90°) during each pursuit, as seen by the observer.

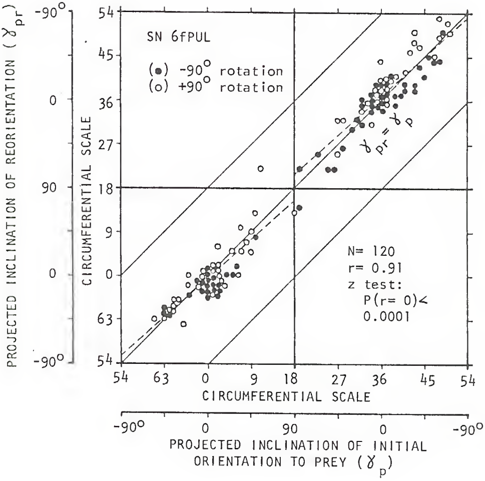


Figure 87. Result of experiment described in Figure 86, for a female *P. pulcherrimus*. The inner scales refer to directions on the F scale shown in Figure 86. The projected value of γ in a vertical plane [plane of observation; Figure 86 (B)] is γ_p; γ_{pr} is the corresponding projection of γ_r. Both the linear regression (dashed lines) and the correlation coefficient (r) are based upon the relationship of γ_{pr} to γ_p. In the absence of visual cues, the spider is able to return to an appropriate radial direction for reorientation. This is attributed to the ability of these spiders to orient with reference to gravity.

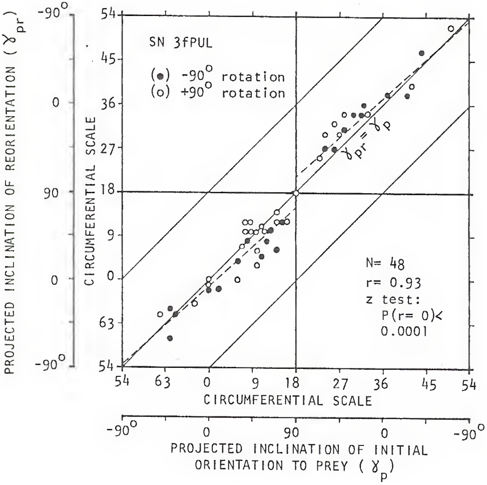


Figure 88. Result of experiment described in Figure 86, for a female P. pulcherrimus. Interpretation agrees with that given in Figure 87.

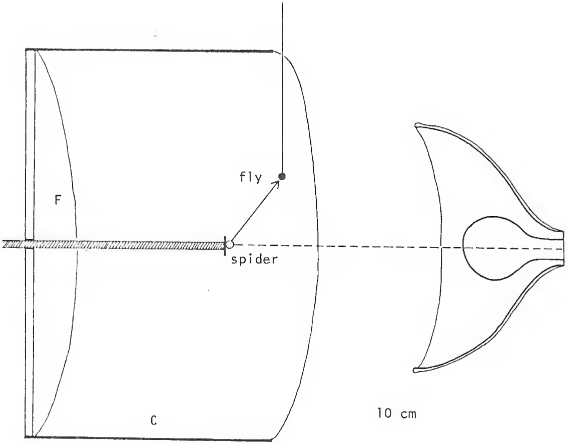


Figure 89. Vertical section, with some perspective added, of the apparatus used in the jump-recovery experiment. A circumferential scale (F) like that shown in Figure 63 is present at the back of a cylinder (C) which eliminates visual cues for the determination of a radial direction from the horizontal axis (dashed line) of this structure. By this scale, an observer in the darkened room behind the centered lamp (at right) can read the radial orientation of the spider to the nearest 10°. The spider waits on a circular, vertical (2 cm diameter) platform at the end of a centered wood dowel, as shown above. The prey is advanced toward the spider along a radius until the spider jumps. Paired data for subsequent analysis (Figure 90) includes the radial orientation of the spider-to-prey vector at the time of the jump, and the radial orientation maintained by the spider after it climbs back to the platform after failing to capture the prey. It is assumed that visual cues for the determination of radial direction are lacking with this arrangement. See also Figure 91.

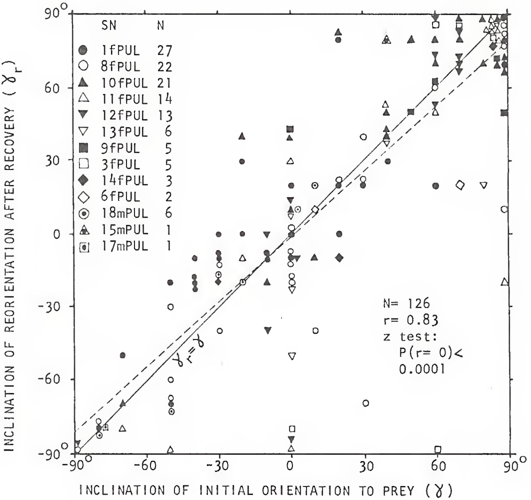


Figure 90. Pooled data (from 13 individual *P. pulcherrimus*, listed at upper left) for the jump-recovery experiment described in Figure 89. The correlation of γ (initial direction of prey with reference to the horizontal, or inclination of prey direction, at time of jump) and γ_r (the direction of reorientation of the spider after recovery from the jump) is highly significant. In addition, when the initial prey direction was to either the right or to the left of the vertical, reorientation was directed toward that same side 84/101 times ($P < 0.001$). Pooling of data was required by the fact that, after missing a certain number of jumps, individuals would only jump when capture was certain, when the prey was so near that it could not be removed fast enough by the observer.

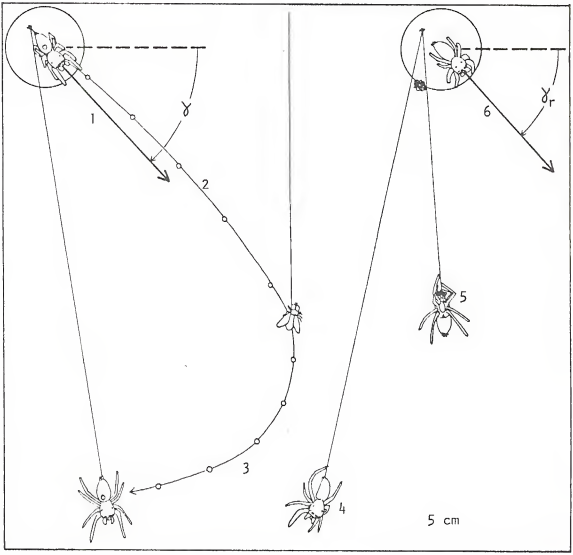


Figure 91. Description of the jump-recovery behavior of Phidippus, corresponding to the data presented in Figure 90. Initially the spider orients (1) toward prey at a particular direction with reference to the horizontal (as indicated by γ). The spider jumps (2), but misses the lure as it is quickly removed by the observer, who must be careful to anticipate the jump of the spider. The spider then swings like a pendulum (3), back and forth, then catches the dragline with a leg IV (4). The spider winds-up the dragline as it climbs (5) to recover to the jumping position, where the wound dragline is discarded. Immediately the spider turns in a reorientation (to prey) direction (6), which is indicated with reference to the horizontal (γ_r). As shown in Figure 90, this apparent reorientation brings the spider to face the original direction of the prey with an appreciable accuracy. Presumably only gravity is available as a reference for the determination of prey direction in this experiment (Figure 89).

Phidippus utilize a generalized ability to orient with reference to gravity in the execution of many behaviors. These spiders can evaluate both the distance (D) and direction of objectives with reference to gravity (γ information), as determinants of subsequent behavior. *Phidippus* can also remember a direction with reference to gravity, and they can employ this γ information in the determination of an accurate reorientation turn after a segment of pursuit. There is strong evidence for the ability of *Phidippus* to compensate for their own movement in the determination of an appropriate direction of reorientation in the gravitational reference system, and this feature of *γ orientation* will be considered in a subsequent section.

SECTION XI
VISUAL REFERENCE TO PLANT CONFIGURATIONS

The role of vision in the evaluation of potential secondary objectives during prey pursuit has already been established. Visual information, with regard to the form or configuration of the local vegetation, can also contribute to the orientation of Phidippus during its pursuit of prey.

In the course of a long, detoured pursuit, reorientation turns are frequently directed toward specific plant configurations which are presumably associated with the prey, and the pursuit continues even when the prey itself is no longer visible, until the plant position of the sighted prey has been attained by the spider. In this sense, then, the plant position of the prey, rather than the prey itself, can serve as the primary objective of directed movement and reorientation during pursuit. This assessment agrees with the fact that the prey is in general much less visible than the plant configuration with which it is associated, and the latter can provide conspicuous and recognizable features for the resetting of the primary objective (the apparent role of reorientation). Direct pursuit of the plant configuration associated with prey is readily demonstrated, particularly when the prey disappears behind a leaf. In response, a Phidippus will often run directly to that leaf which is blocking its view, and it will then move slowly to an edge of this obstruction to peer into the space behind the leaf; the functional significance of this "cautious" approach lies not only in the advantage of not giving alarm to a potential prey (the equivalent of stealth), but also in the advantage of detecting a potential adversary before revealing much of one's own presence to that adversary.

Since Phidippus can potentially utilize a continuous visual reference to the immediate surroundings, as well as the more directed application of vision to the primary objective (reorientation), during the pursuit, the question of the extent of the ability of these spiders to recognize specific forms is of great importance. In the pursuit described in Figure 92, information analygous to the following statement may be recorded by the spider during its initial orientation to the prey (1): A potential prey is out on that branch. Since, in this particular problem of access, there are no other branches in the vicinity to be confused with the objective branch, a relatively simple evaluation of the form of the branch should suffice. The ability to recognize a particular configuration by its form implies the existence of an ability to retain an internal impression, or memory, of specific features which characterize that form. If the set of features which comprise this memory contains more than a single sign stimulus, such as color, associated with the object, then the animal may be using a functional analog of that which we term a concept, in the anthropomorphic sense of the term. This major question, of the nature of the concept-equivalents (complex feature recognition) which can be employed by the salticid as it deals with its local environment, deserves a great deal of study. With regard to oriented movement upon vegetation,

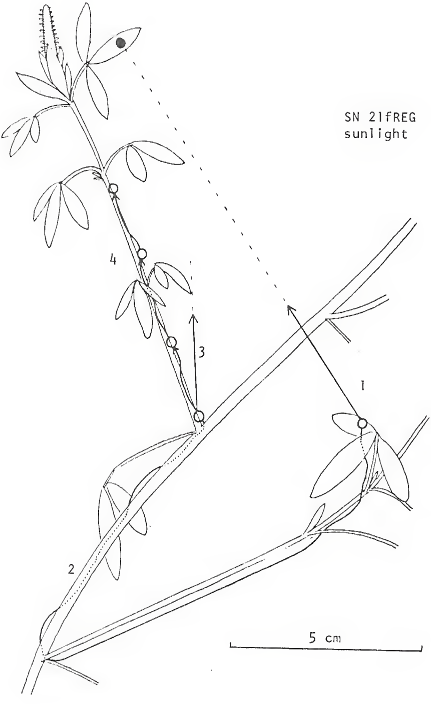


Figure 92. Detoured pursuit by a female P. regius. After the initial turn to the prey (standard lure; 1), the spider runs a long, non-stop detour (2) prior to reorientation (3). It appears that Phidippus can orient visually to the elements of the local plant configuration during the course of a long, uninterrupted run of this sort.

the nature of those concept equivalents which can be applied to the form and configuration of plants is of particular importance.

The specific appearance and arrangement of leaves or groups of leaves should change greatly with the movement of the spider; thus visual criteria for the recognition of an objective should be somewhat generalized. In the pursuit shown in Figure 93, the spider reorients to the *wrong* objective after a long, winding run. Nonetheless the pursuit of this new objective agrees with the initial association of the prey with a *leaf*. This error is also consistent with the use of gravity as a reference (γ information): The spider which runs down from the level of the sighted prey in pursuit should then look up to relocate that prey. Clearly the route itself, which is not straight, could not provide reliable θ information for this spider. It is significant that distinct, and smoothly executed, reorientation turns are directed toward *each* of the near configurations which satisfies the initial association of prey with a leaf of this plant, prior to the continuation of pursuit. In the pursuit shown in Figure 94, the spider appears to employ a directed visual survey of the local plant configuration to reestablish the objective of its pursuit, before it ventures out onto the branch associated with the prey. As in many situations which might be encountered by a spider upon a real plant, there is little ambiguity here to interfere with this recovery of orientation, provided the spider can recognize a branch in some way.

There is no doubt that *Phidippus* can use their vision continuously as they are moving (Figure 21). One can demonstrate this fact quite simply by chasing the animals upon a surface. *Phidippus* can also

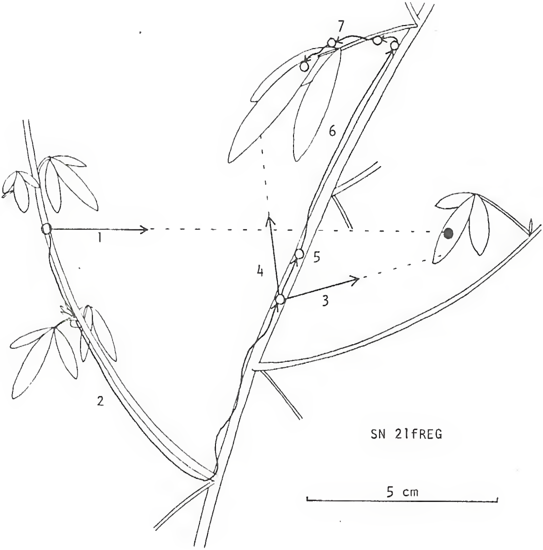


Figure 93. Choice of the wrong objective by visual survey. After the initial orientation (1), this female P. regius quickly completed a climb down the underside of a branch coupled with a winding ascent of the stem (2), before stopping to reorient. After 2 discrete turns (3 and 4) toward separate leaves, the spider apparently selected the object of the second turn as the objective of subsequent pursuit (5-7). A number of errors of this kind have been recorded for individual P. pulcherrimus and P. regius, each involving the pursuit of a leaf or stem similar in appearance to the correct objective.

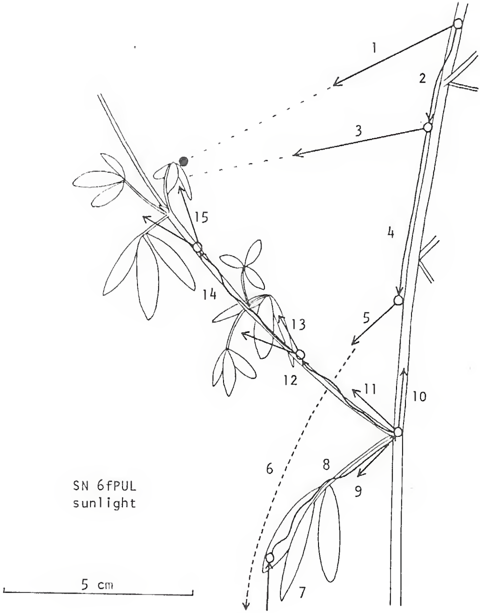


Figure 94. Apparent visual recovery of the primary objective after a fall, during an indirect pursuit by a female P. pulcherrimus. After the initial orientation to the prey (1), the spider walks slowly (2), reorients (3), again walks slowly (4), turns to the side branch (5), apparently missing a jump to the same (6). The spider climbs the dragline to a leaflet of the plant (7), then (8) returns to the main stem to perform a series of large survey turns (9-11) prior to continuation of the pursuit (12-15).

orient to configurations near the immediate route when moving. This can be observed when the spider moves directly toward a secondary objective (Figures 4, 95), apparently guided in this approach by continuous visual feedback from the objective. This visual guidance along the course of the immediate route is most evident when the spider reaches out, or jumps, in the direction of its continuing route of access. The running salticid can visually anticipate a forthcoming reach for an object, or the necessity to avoid an obstacle in its path.

The visual experience of the salticid can play a significant role in maintaining an accurate memory of prey position during pursuit, by providing information which can be used to correct a reorientation turn and reset the course toward a recognized configuration. Vision also provides information which may, in certain circumstances, be required for the determination of the reorientation turn itself.

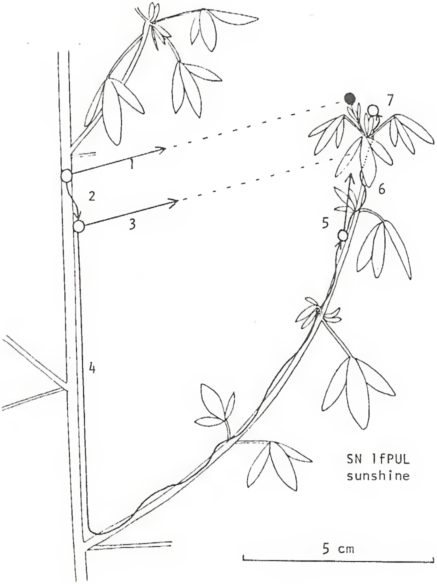


Figure 95. Detoured pursuit by a female P. pulcherrimus. Typically, a descent toward a primary or secondary objective takes place on the side of the stem facing that objective, as shown here (4). It appears that the constant radial orientation of the spider on the main stem is maintained by continuous visual reference to this secondary objective. Continuous visual survey of the route is most clearly demonstrated when the spider successfully jumps from position to position along an interrupted route, but it may also be seen in the deliberate reach of the spider for a side branch prior to actual physical contact during a circuitous approach like the one shown above.

SECTION XII
VISUAL DETERMINANTS OF THE REORIENTATION TURN (RADIAL ORIENTATION)

Directions which might be specified visually can, as a convention, be separated into two independent components: An angle with reference to the direction of movement (θ), and a radial direction which is perpendicular to that direction of movement (radial orientation). This distinction is probably appropriate for several reasons. Phidippus can follow θ information in preference to conflicting visual cues beyond the immediate route (Figures 39-41), a behavior which is consistent with the fact that the visual experience of the route by the spider is generally fairly constant and dependable as a reference direction, whereas near configurations to the side of that route move considerably relative to the position of the moving spider. In fact, the spider would require θ information even in this case, just to appraise the relative movement of the configurations that might be used to provide the equivalent of θ information.

In the determination of a θ-independent direction, however, visual references beyond the immediate route can be quite useful. The θ-independent component of visual orientation specifies a direction in the plane perpendicular to the direction of movement by the spider, or a radial direction with reference to the route. This component provides a reference which remains constant during the movement of the spider, and no compensation for movement is required: Since the combination of prey position (a point) and the route itself (a line) specify a unique plane in space, the prey position always remains in the same radial direction relative to the direction of movement. Only when the spider is required to determine a radial direction from a completely vertical route is this component also independent of gravity (γ) information, as shown in Figure 113 (below).

For this reason the vertical cylinder shown in Figure 96 was designed, to evaluate the ability of Phidippus to employ a visual cue to determine the radial component of reorientation from a vertical route. Although both θ and γ information are available, neither can contribute to the determination of a particular radial direction in this situation. As indicated by the results of this experiment (Figures 97-99), Phidippus can utilize a simple vertical stripe as a visual reference to determine a radial direction from the route. In the absence of visual cues to this effect (the control experiment), the radial direction of reorientation is remarkably inaccurate. Only the initial reorientation direction is recorded in this experiment. In fact, in the absence of visual cues, individuals often circle the vertical bar in a succession of turns, apparently in a futile attempt to relocate the radial direction of the prey. This behavior is not observed when the visual cue (vertical stripe) is present.

Under natural conditions, Phidippus can generally maintain an accurate radial orientation after a long, winding ascent of a plant stem (Figure 100). The apparatus described in Figure 101 was designed for the evaluation of the role of different visual reference systems in the determination of the radial direction of reorientation by Phidippus

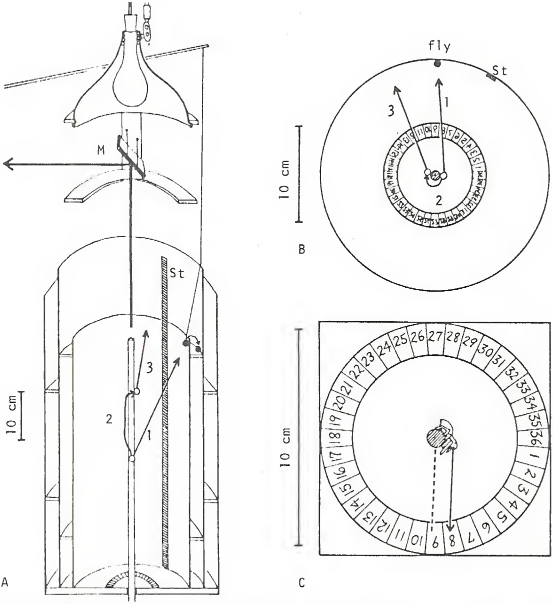


Figure 96. Apparatus for measurement of the accuracy of radial reorientation after a vertical ascent in pursuit of prey. A: Vertical section of the apparatus, with added perspective. The spider (open circles) runs the pursuit on a vertical bar (9 mm wood dowel) at the center of a double cylinder constructed of white paper. The pursuit consists of the initial orientation (1) to the lure (solid dot), an ascent (2), during which the lure is concealed as shown, and a reorientation (3). A 1 cm wide green paper stripe may be placed into the cylinder as shown (St) to determine its ability to facilitate the accuracy of reorientation in a radial direction. The large arrow indicates how an observer standing to the side of the cylinder, out of view by the spider, can view the pursuit with the mirror (M). B: View of the bottom of the cylinder as seen from above, showing the position of the vertical stripe (St) 30° to the side of the prey direction. C: Observer's view of a radial orientation as seen in the mirror. The axial direction faced by the spider (dashed line; in this example, 9) is recorded as accurately as possible.

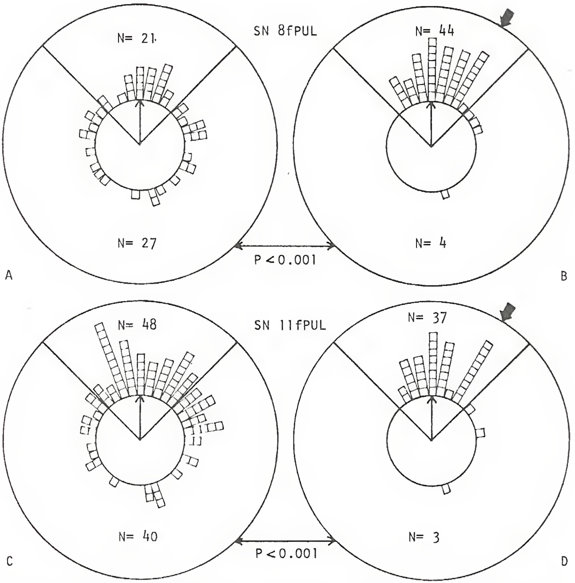


Figure 97. Accuracy of radial reorientation in an unmarked vertical cylinder (A and C; Figure 96), and in that cylinder with a vertical stripe situated 30° to the right of the prey position (B and D), for two female P. pulcherrimus. For each set of trials (A-D), the direction of the prey, as viewed from above, is indicated by a short arrow at the center. Each square represents a reorientation in that particular direction from the center. In (B) and (D), the arrows at upper right indicate the position of the vertical stripe on the cylinder. As indicated above, reorientations are partitioned into those involving less than a 45° deviation from the prey direction (upper quadrant), and all others. For each spider the controls (left) are compared with the cued (vertical stripe) trials (right) with a 2 X 2 contingency table of these partitioned results. Respective P values (null hypothesis) are given above. This simple analysis allows one to conclude that a significantly greater proportion of the reorientations deviate by less than 45° from the prey position when a vertical stripe is available as a visual cue.

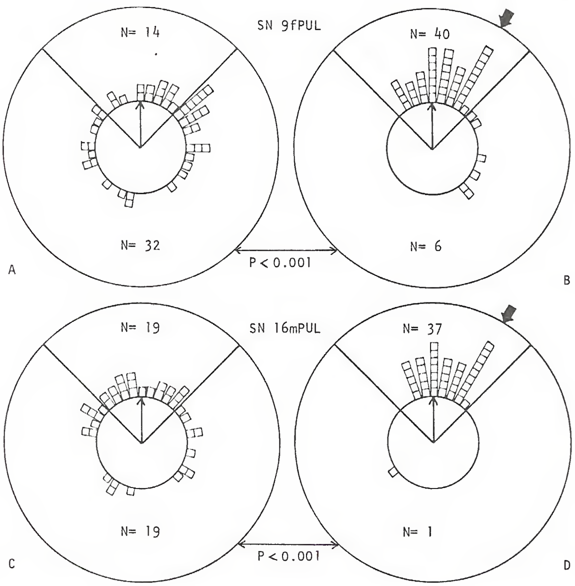


Figure 98. Accuracy of radial reorientation by two individual P. pulcherrimus in a vertical cylinder, with (left) no pertinent visual cues, and (right) with a vertical stripe present as indicated by the arrow at upper right. Analysis of these data is consistent with that given in Figure 97.

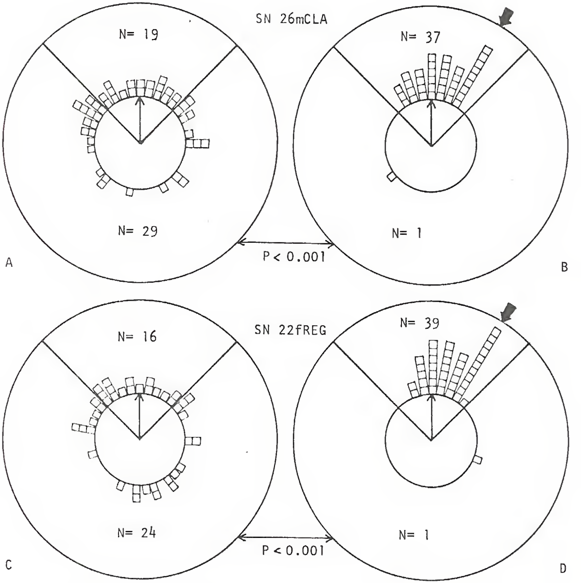


Figure 99. Accuracy of radial reorientation in a vertical cylinder by a male P. clarus (A and B) and a female P. regius (C and D), with and without a vertical stripe to provide a visual cue. Analysis of these data is consistent with that given in Figure 97.

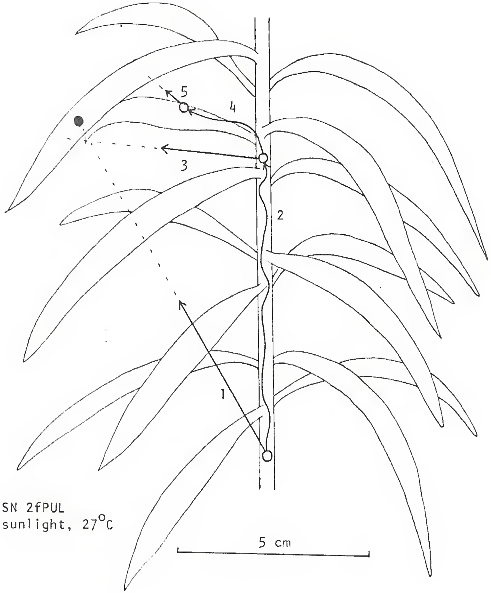


Figure 100. Pursuit on the main stem of *Solidago* by a female *Phidippus pulcherrimus*. These spiders have little difficulty, in nature, in maintaining an accurate radial orientation (as indicated by reorientations 3 and 5, above) after a long ascent (2) of a vertical main stem. Neither θ nor γ can provide the requisite reference system for this memory of prey position.

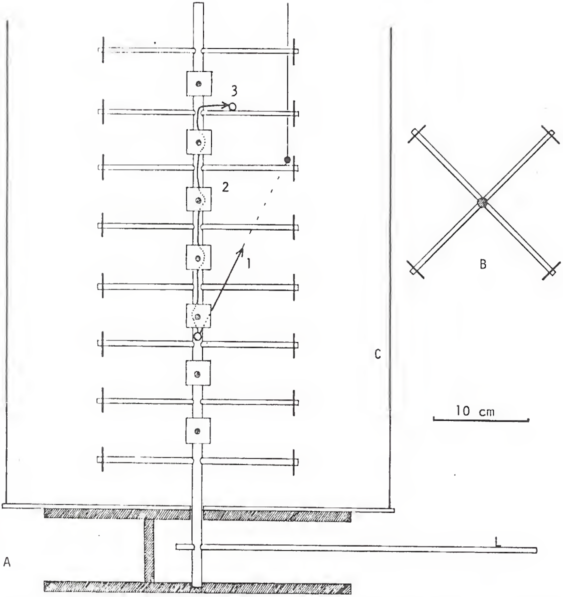


Figure 101. The rotating plant projected onto vertical (lateral view; A) and horizontal (view from above; B) planes. As shown in (A) the plant is surrounded by a cylinder of heavy white paper, which can itself be rotated during the pursuit run. A lever (L) permits rotation of the plant (± 90°) during pursuit. In each trial, the spider is first shown the standard lure in 1 of 4 radial directions corresponding to the direction of the branches as shown in (B). After this initial orientation (1), the spider runs a necessarily winding ascent (2) and then reorients (3) in, generally, 1 of the 4 radial directions. At times the spider will reorient in a radial direction perpendicular to the radial direction of the branch on which it rests. Each pursuit begins with the spider on the stem as shown, at least 2 rungs (or 12 cm) below the level of the prey (lure) position. At the initiation of pursuit, the lure is immediately removed, and the respective rotations of either the plant or the cylinder are completed before reorientation.

during pursuit. The configuration of this artificial plant is radially symmetrical in horizontal projection [Figure 101 (B)], allowing the spider, which in general reorients toward one of the branches associated with the prey, a choice of four radial directions (quadrants) in the context of a certain amount of visual ambiguity. This ambiguity (identical branches facing in each direction from the stem) is necessary to avoid the generalized recognition of a branch by Phidippus (discussed in the preceding section) as the sole determinant of radial orientation.

Even when this plant is rotated within a uniform, closed cylinder during the pursuit (Figure 102), Phidippus can maintain an accurate radial orientation with reference to the plant itself (Table 5). This result can be compared with the inability of these spiders to determine a radial direction from a vertical rod when no visual cues are present: With the artificial plant (Figure 101), a significantly greater fraction (177/210 for P. pulcherrimus) of the reorientations are directed toward the correct quadrant than in the control situation (A and C in Figures 97-98; 102/220; $P < 0.001$), where no radial visual cues are available to the spider. Actually, when the branches are present, the reorientation turns are not only directed toward the correct quadrant, but they are also directed in a specific direction indicated by one of the branches. This agrees with the notion that the prey is associated with a branch by the spider. It should also be noted that Phidippus can maintain this radial orientation from the stem, regardless of the fact that the pursuit may involve more than a 30 cm ascent, and that the course of this ascent necessarily winds around the stem to avoid the obstacles posed by the attachment of branches.

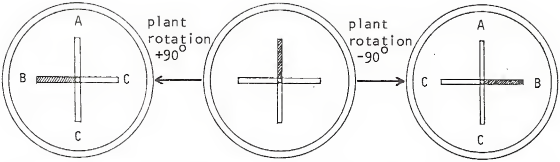


Figure 102. Diagram of control rotation of the plant within the white cylinder, as viewed from above. As in subsequent experiments, the results are essentially the same whether the rotation is +90° or -90°. Since virtually the same number of trials are run for each spider with the rotation in either of the two directions, the results are pooled in a manner consistent with the symmetry of the two problems, as indicated by the letters (A-C) shown above. As a convention, the direction of the initial orientation to prey is always to the top of the page in each diagram (with reference to a fixed, external system); the radial direction of that branch corresponding to the initial orientation is shaded. Possible results, by category, are:

A: Fixed reference. Reorientation follows the original direction of orientation irrespective of the rotation of the plant.

B: Orientation with reference to the plant itself, irrespective of its rotation. The radiating branches provide a potential reference system for the visual determination, or following, of a particular radial direction. This alternative is also consistent with the kinesthetic experience (for idiothetic control) of the spider.

C: Other results, presumably due to error or loss of orientation.

Table 5. Results of the control rotation of the plant within a closed cylinder, according to the categories given in Figure 102.

SN	N	A	B	C
8fPUL	60	4	44	12
9fPUL	30	2	27	1
11fPUL	60	2	52	6
15mPUL	60	2	54	4
total PUL	210	10	177	23
26mCLA	40	1	37	2

Category (B) clearly dominates in a significant ($P < 0.001$) majority of the trials for each spider; the plant itself provides the reference system for the determination of radial direction for reorientation, in conjunction with the experience of the spider (kinesthesis) upon that plant.

The data and analysis of a series of similar experiments presented in Figures 103-107, along with the corresponding Tables 6-11, demonstrate clearly that background visual patterns, including variation in light intensity, can also contribute to the radial orientation of *Phidippus*. When the two are in conflict, the spiders follow *either* the immediate plant configuration *or* the background in these trials, presumably as dictated by the direction of the branches. One individual (Table 9, SN 15mPUL) did orient in an intermediate direction at times, between that specified by its experience upon the plant and that specified by the background. This result is unusual, as it is inconsistent with the association of the prey with a particular plant configuration (branch) by the spider.

The use of background visual patterns, or relatively fixed visual references at a distance which do not move appreciably as the spider moves, to establish a radial direction compares with the general phenomenon of photomenotaxis, as it is observed in the behavior of other spiders, including the araneid *Araneus diadematus* (Peters, 1932) and the agelenid *Agelena labyrinthica* (Bartels and Balzer, 1928; Bartels, 1929; Görner, 1958, 1966; Dornfeldt, 1975a, 1975b).

A related experiment designed as a potential demonstration of the use of the pattern of polarized light in blue sky directly above the spider to determine a radial direction from the ascending (vertical) route of pursuit is described in Figure 108. As the results (Table 12) indicate, these spiders, irrespective of plant rotation, orient exclusively with reference to information provided by their immediate experience on the plant configuration, as if the information available in patterns of sky polarization did not exist. In this experiment, the

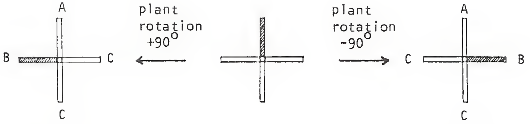


Figure 103. Diagram of rotation of plant in an open room, with the lamp directly overhead, as view from above. As in the control (Figure 102), comparable results for both +90° and -90° rotation have been pooled into the following categories:

A: Fixed reference, presumably external to the plant. Since few of the control reorientations were in this direction, it follows that reorientation in this direction should constitute the use of background visual patterns (not available in the control) by the spider to determine a radial direction.

B: Orientation with reference to experience upon the immediate plant, irrespective of its rotation. This was the predominant result in the control experiment.

C: Other results.

Table 6. Results of rotation of the plant in an open room, according to the categories given in Figure 103.

SN	N	A	B	C
8fPUL	60	40	18	2
9fPUL	22	13	9	0
11fPUL	60	16	44	0
15mPUL	60	18	39	3
total PUL	202	87	110	5
26mCLA	40	17	23	0

For each spider, category (A) is significantly ($P < 0.01$) larger than in the control (Table 5). Since the lamp remains overhead, visual patterns beyond the plant itself, in the background, are apparently being utilized to establish a radial direction for reorientation in a significant number of the trials. This appears to apply more to some individuals (such as SN 8fPUL), than to others.

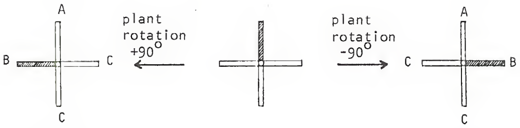


Figure 104. Diagram of rotation of the plant with the cylinder removed. As in earlier experiments, the possible results for both +90° and -90° rotation are consistent, and these have been pooled into the following categories:

A: Fixed reference, provided by either background visual patterns or by the pattern of illumination of the plant itself.

B: Orientation with reference to experience on the immediate plant, irrespective of its rotation.

C: Other results.

Table 7. Results of rotation of the plant in an open room, when illuminated by a lamp at an angle of 45° to the axis of the plant.

SN	N	A	B	C
8fPUL	60	44	15	1
11fPUL	60	36	22	2
15mPUL	60	40	20	0

This arrangement not only provides a strong directional cue in the form of the lamp itself; it also illuminates the plant in a highly directional pattern of shading (Figure 104). Both SN 11fPUL and 15mPUL have a significantly ($P < 0.01$) greater number of reorientations in the (A) category as compared to the situation with overhead lighting in the open room (Table 6). In all cases, (A) is more frequently the result than in the control (Table 5; $P < 0.01$).

Table 8. Results of rotation of the plant in directional (near 45°) sunlight under a blue sky, according to categories given in Figure 104.

SN	N	A	B	C
8fPUL	63	59	4	0
11fPUL	49	29	18	2

In both cases, (A) is significantly more frequent a result than in either the control (Table 5) or open room situations (Table 6; $P < 0.01$) for these individuals.

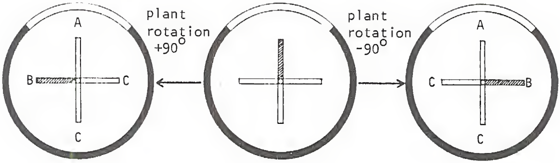


Figure 105. Diagram of the experimental rotation of the plant (as shown in Figure 101) within a cylinder containing 1 white quadrant and 3 black quadrants. An incandescent lamp is directly overhead. As shown at center, the prey always appears in the white quadrant. Pooled categories for potential results are:

A: Fixed reference, presumably using the white quadrant an an indicator of the radial direction of the prey.

B: Orientation with reference to immediate experience upon the plant, irrespective of both rotation and the background pattern.

C: Other results.

Table 9. Results of rotation of the plant during pursuit within a marked cylinder, as described in Figure 105.

SN	N	A	B	C
8fPUL	77	35	40	2
15mPUL	80	22	58	0

As compared with the control (rotation in a unmarked cylinder; Table 5), (A) occurs a significantly greater number of times. This can be attributed to the association of the radial direction of the prey with the white quadrant by the spider ($P < 0.01$ in each case). For SN 15mPUL, 4 intermediate reorientations have been omitted from this analysis, with no effect upon the results. Most individuals always orient distinctly toward one of the four directions specified by the pattern of the branches of this plant.

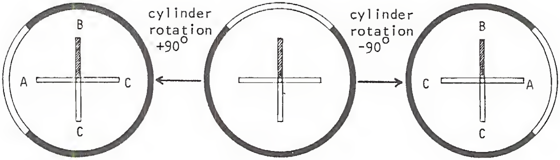


Figure 106. Diagram of the experimental rotation of the patterned cylinder during the pursuit. The plant remains in a stationary position. As in the previous experiment, the prey appears in association with the white quadrant (center, above). Categorical results are:

A: The spider reorients with reference to the white quadrant, presumably associated with the prey direction, irrespective of its rotation.

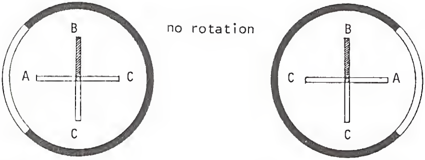
B: The spider orients either with reference to a fixed direction, or with reference to its experience upon the plant.

C: Other results.

Table 10. Results of rotation of the background cylinder during pursuit, as described in Figure 106.

SN	N	A	B	C
8fPUL	65	26	37	2
11fPUL	65	22	42	1
15mPUL	61	9	52	0

Although (B) is the predominant result, (A) occurs significantly more often ($P < 0.01$) than (C) for each spider. Thus one can conclude that the spider will follow the white quadrant in preference to the direction indicated by the immediate plant configuration a significant number of times, and this result is not due merely to chance error.



fly to the right of the white quadrant

fly to the left of the white quadrant

Figure 107. After completion of the trials shown in Figures 105 and 106, prey was presented in black quadrants bordering the white quadrant on either side, as shown above. This was done to check for the possibility that the spiders would tend to reorient in the direction of the white quadrant irrespective of the prey position, a factor which would make the interpretation of data presented in Tables 9 and 10 meaningless. Pooled categories of potential results are:

A: Reorientation in the direction specified by the white quadrant, irrespective of the fact that the prey originally appeared in a black quadrant.

B: Reorientation in the appropriate direction of the prey, as specified by both background and plant configuration.

C: Other results.

Table 11. Results of the control experiment described in Figure 107.

SN	N	A	B	C
8fPUL	60	2	56	2
11fPUL	65	2	60	3

There is no significant tendency for the spiders to reorient toward the white quadrant, irrespective of the position of the prey. Therefore the interpretation of results in Tables 9 and 10 is probably a valid one: The spiders can associate the position of the prey with a background pattern of illumination, in determining an appropriate radial direction of reorientation from a vertical stem.

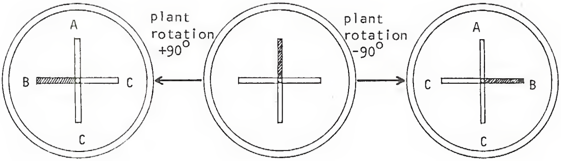


Figure 108. Diagram of rotation of the plant within a uniform white cylinder, under a clear blue sky. The sun was blocked by the observer and a wall to the west of the apparatus; the solar altitude varied from 30° to 5° during the course of the experiment. During each initial sighting of the prey (see Figure 101), the spider had a clear view of blue sky in the background, at the zenith. Results are placed in the following categories:

A: Reorientation based upon the use of a fixed external reference system. This might consist of the polarization pattern of the blue sky directly above, or it could involve, at least in part, the use of either the wall or observer to one side of the apparatus (which block the sun) as a reference for direction.

B: Use of the immediate plant configuration or visual and kinesthetic experience upon the plant, irrespective of its rotation.

C: Other results.

Table 12. Results of the experiment described in Figure 108.

SN	N	A	B	C
11fPUL	91	5	75	11
15mPUL	72	4	59	9

The results shown here do not differ significantly in any way from those obtained in the control (Table 5) for the same individuals. Again, (B) is the predominant result, and the level of (A) events is remarkably consistent with the noise level of (C) events, with no evidence for any significant occurence of (A). In this situation, the spiders rely upon their experience upon the immediate plant configuration to establish a radial direction, irrespective of its rotation during the pursuit.

spider initially sights the prey as a silhouette against a background of blue sky, at the zenith (low solar altitude), in each trial. Yet no indication of the use of the pattern of sky polarization could be discerned. Several additional experiments of a similar design, for which data are not given here, also support the hypothesis that polarized light patterns do not contribute to the orientation of *Phidippus* during its pursuit of prey. An apparatus comparable to the vertical cylinder described in Figure 96 was placed, alternately, under both blue sky and a polarizing filter beneath an incandescent lamp. In both cases the spiders tended to error greatly in their reorientation after ascent toward the prey, although admittedly the incandescent lamp is probably deficient in critical wavelengths for this purpose.

This negative result does not conform with the demonstration of astromenotaxis, based upon patterns of sky polarization, in other spiders, including the agelenid *Agelena labyrinthica* (Görner, 1958, 1962, 1966), lycosids of the genus *Arctosa* (Papi, 1955, 1959; Papi, Serretti, and Parrini, 1957; Papi and Syrjamaki, 1963; Papi and Tongiorgi, 1963), and the theraphosid *Eurypelma* (Henton and Crawford, 1966).

Both the PME and AME of *Arctosa* exhibit an electroretinographic response to rotation of the plane of polarized light, although only the AME are actually required for orientation with reference to the polarization pattern by these animals (Magni, Papi, Savely, and Tongiorgi, 1962, 1964, 1965). The receptors of the AME of *Agelena* which appear to be structurally capable of responding to polarization are situated ventrally where they should receive light from the sky above the spider (Schröer, 1976). With respect to salticids, Land (1969a) suggested that the AME may similarly contain receptors capable of detecting patterns of polarization, although there is no behavioral or physiological evidence to this effect. If, indeed, the salticid AME can be used to perceive the polarization pattern of skylight, then the experiments described above should have been particularly appropriate for the demonstration of this ability, since the sky (or pattern of polarization) was directly in line with the vision of the AME during both orientation and pursuit.

It is possible that the specialization of the salticid AME for purposes of high resolution (form vision) has taken precedence over the potential role of these eyes in the detection of polarization patterns. In this regard, the AME have a very restricted field of vision in salticids, as compared with other spiders, and they are not often directed toward the sky during a pursuit. As noted earlier, these spiders tend to face down on a stem waiting for prey, and to pursue prey which is below this waiting position, without the use of turns directed toward patches of blue sky to determine a radial orientation during pursuit.

Of course there is always a possibility that there are some unrecognized applications of information provided by the pattern of skylight polarization to the behavior of Phidippus, particularly since this information appears to be utilized by other spiders. Nonetheless it is reasonable to conclude that information provided by the immediate plant configuration, at least, is considerably more relevant to the behavior of Phidippus during the pursuit of prey.

Whether escaping from a potential adversary (Figure 109), or conducting a pursuit of prey, Phidippus can utilize visual information,

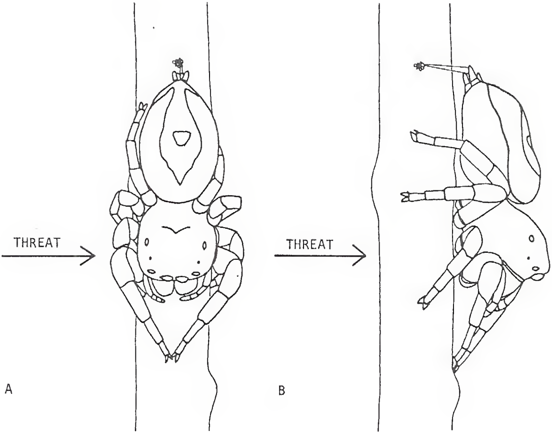


Figure 109. Rapid escape response to a visual stimulus, for a female *P. pulcherrimus* in a waiting position on a vertical stem. When a potentially dangerous (threatening) simulus appears in the visual field of *Phidippus* (A), the spider can rapidly step to the opposite side of the stem as shown here (B), to a concealed position. These spiders often rest with legs hooked over the edge of a leaf, as if in preparation for a rapid move to the opposite side of that leaf, if necessary. In a general sense, with reference to the behavior on a stem shown above, this is an example of radial orientation with reference to visual information. This response was observed for an immature *P. princeps* when it noticed a large, metallic blue wasp flying by at a distance of 1 m.

provided by either the form or intensity of its visual experience, to determine a radial orientation to a vertical stem. An appropriate reorientation direction may be specified by visual information derived from elements of either the local plant configuration, or more distant background patterns, which can be remembered and subsequently recognized by the spider. In this regard, there is no reason to believe that patterns of sky polarization are of any use to the salticid during the pursuit of prey. Differences in background light intensity may, however, be of considerable importance; it is quite possible that *Phidippus* might employ an ability to evaluate patterns of reflected polarized light, as well as light intensity, in their evaluation of the appearance of surrounding vegetation.

SECTION XIII
ORIENTATION IN THREE DIMENSIONS

Three different reference directions which can be used by Phidippus to maintain a memory of prey position during pursuit have been examined: the direction of movement along the immediate access route (θ orientation), the force of gravity (γ orientation), and a direction perpendicular to the direction of movement which is specified by visual information (radial orientation). Short-term memory of the prey position has been demonstrated within the context of each of these reference systems, independently, by the isolation of each system in turn.

Nonetheless, even in the preceding experiments, Phidippus were orienting in three-dimensional space. The ability to specify a relative position in space requires the use of at least two independent reference directions (they need not be perpendicular) to specify direction, in addition to an appraisal of prey distance.

Thus, even when the reorientation direction is measured within a single plane, in the study of an isolated reference system, at least one additional reference direction is also used to specify the direction of reorientation in space. As an example, the horizontal bar (Figures 67, 68) can be used for the study of θ orientation in the horizontal plane, but only because both γ and visual (radial) information which are available to the spider in this situation specify the same horizontal plane to begin with.

There is no question, then, but that *Phidippus* can orient successfully in space, utilizing at least two independent (and spider-centered) reference systems in concert for the specification of a reorientation direction. Since only two reference directions are required to determine a direction in space, the use of at least three systems by these spiders for this purpose demands some explanation.

As shown in Figure 110 (A), θ orientation and radial orientation are always independent, and by themselves they are always sufficient to determine a unique direction in space, independent of any gravity-referenced information. One could develop a rationale for the use of gravity, nonetheless, based upon the complete reliability of its vector. Gravity (γ) information might allow the spider to maintain an orientation when all of the local visual cues are ambiguous, or where the access route is so irregular that θ information cannot be relied upon. This might apply in particular to situations where the spider is moving on a horizontal route, surrounded by vegetation, where background visual patterns are constantly changing. In a strict sense, however, γ information is not required when both θ and radial (visual) cues are adequate.

As shown in Figure 110 (B) and (C), both θ and radial orientation may be required in certain situations. Granted that γ information is always available, and is probably utilized in most if not all situations, an additional reference direction which can provide some γ-independent information is also required. In this regard, θ information becomes more important and finally indispensable as the direction of movement approaches the horizontal (B). As the route becomes more vertical (C), radial orientation similarly becomes more critical to the

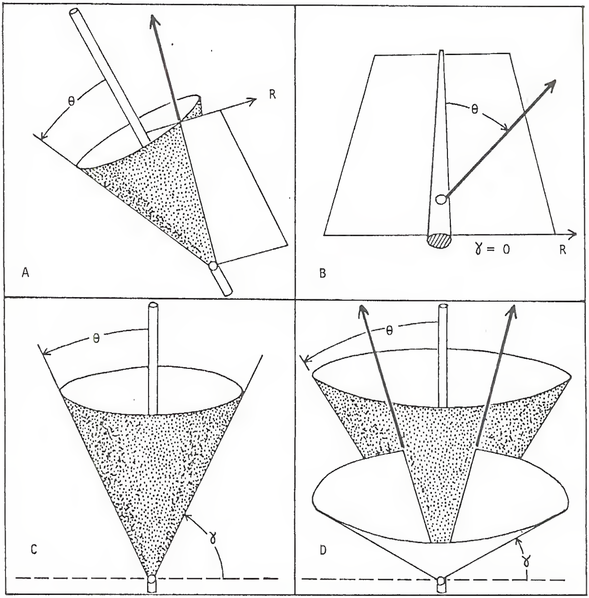


Figure 110. Complementarity of reference systems for orientation. A: Irrespective of the orientation of the route with reference to gravity, θ and a radial direction (R) with reference to the route always provide the necessary two reference systems for the determination of a unique direction in space (large arrow). B: When both the prey and the route are situated in a horizontal plane, γ and R provide the same information, and θ is required to determine a direction. C: When the route is vertical (or near vertical) θ and γ provide the same information. Here R is required to define a unique direction. D: When the route deviates from the vertical (this is an oblique view from above), two directions (large arrows) are defined by a particular combination of θ and γ. Either R, or a sense of "handedness" (which definitely does exist), is required to resolve the ambiguity.

determination of a unique direction in space. As long as the route deviates significantly from the vertical (D), the combination of γ and θ information will suffice.

An interesting feature of many *segments* of pursuit, such as that described in Figures 111-112, is the fact that the route of the spider may be alternately horizontal and then vertical during the course of the run. Successful reorientation after a pursuit of this sort (as shown in Table 13) should require the use of both θ and radial orientation at different times, to act in concert with the γ information. It appears that *Phidippus* can transpose information between the two gravity-independent systems without difficulty, during a single segment of pursuit prior to reorientation. The relative stability of the omnipresent γ reference system during the pursuit, irrespective of the problems (such as transposition) posed by an indirect, curving pathway amid plant configurations of changing appearance, without doubt contributes greatly to the ease with which these spiders can maintain a memory of the prey position in space.

Figures 111-113 and Table 13 provide a simple demonstration of the ability of *P. pulcherrimus* to compensate for movement in space, presumably utilizing at least two independent reference systems simultaneously, to determine an accurate direction of reorientation. An even simpler demonstration and analysis of *movement compensation* is presented in Figures 114 and 115. As noted earlier, radial orientation is only required if the route is completely vertical; in all other situations reference to γ and θ alone will suffice to determine a direction in space, given a certain handedness on the part of the spider which has been demonstrated to exist. In any case, radial

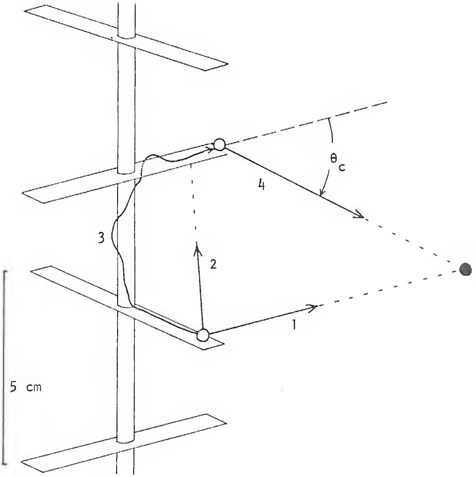


Figure 111. Demonstration of compensation for movement in the determination of a reorientation direction, in three dimensions: perspective drawing of apparatus. Note that θ information may be utilized for reorientation (4), whereas radial (visual) orientation is required during the ascent (3). An ability to transpose between these two gravity-independent reference systems during the pursuit is required for accurate reorientation, a fact which suggests the underlying relatedness of all forms of orientation used by the animal. After the initial orientation to the prey in a horizontal plane (1), many individual Phidippus will make a distinct turn toward the secondary objective shown here (2), and will move to that secondary objective (3). An appropriate direction of reorientation (4) from the new position should be both down and to the right in this situation, to compensate for the movement of the spider. As an experiment, this problem is posed repeatedly to individuals which will run the detour as shown above. The direction of reorientation (4) is recorded for each trial in the simple manner described in Figure 111. In each trial, the prey (standard lure) is immediately removed at the onset of each run. The artificial plant shown here consists of a series of horizontal green paper leaves skewered on a vertical wood dowel (4.5 mm diameter).

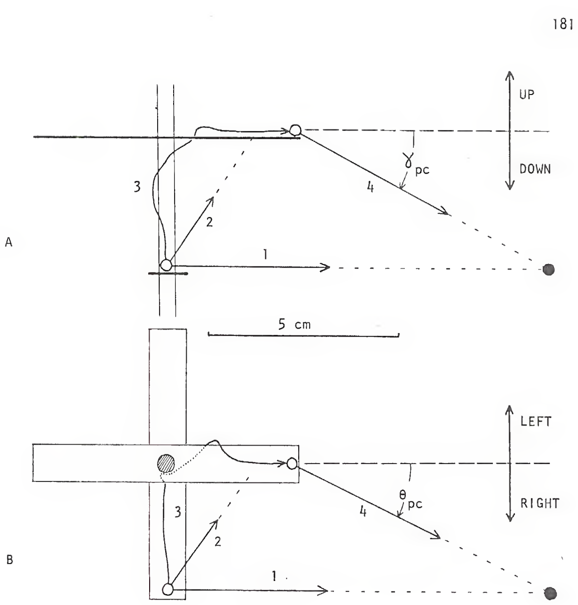


Figure 112. Vertical plane (A) and horizontal plane (B) projections of the detoured pursuit described in Figure 110. Two components of the reorientation turn are shown (A and B), as they are recorded. A: γ_{pc} is the appropriate angle of reorientation (compensated for movement) with reference to the horizontal (inclination), projected onto a vertical plane. B: θ_{pc} is the appropriate angle of reorientation (compensated for movement) with reference to the direction of the immediate route, as projected onto a vertical plane. This represents the gravity-independent component of reorientation. When the spider has attained the reorientation position, the direction of reorientation is recorded with reference to the horizontal (A) in a simple manner, by observing whether the spider turns distinctly up, down (compensated for movement), or an intermediate direction. Similarly, the direction of reorientation with reference to the direction of the immediate route (B) is recorded as being either distinctly to the left, distinctly to the right (compensated), or intermediate. Both right- and left-handed versions of this problem are presented to the spiders, as shown in Figure 112; the results are given in Table 13.

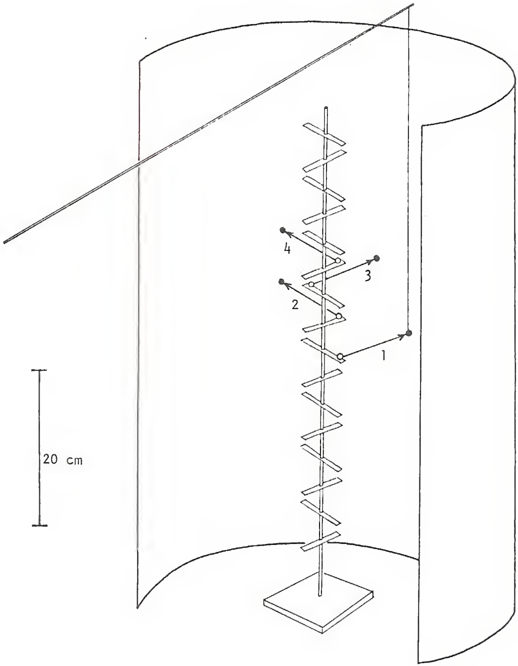


Figure 113. Perspective drawing of apparatus used to demonstrate compensation for movement in the determination of a reorientation direction by the spider. As shown above, the spider can be run through a succession of trials (1-4) as it ascends in pursuit, with the reorientation position of one trial serving as the starting position for the subsequent trial. The artificial plant is placed inside a partial white paper cylinder, as shown above, to remove background cues apart from those afforded by the plant itself, and to increase the visibility of the prey.

Table 13. Results of the compensation experiment described in Figures 110-112. As described in Figure 111, the direction of reorientation was determined for each trial in which a *P. pulcherrimus* completed the indirect pursuit of the secondary objective. Many individuals would not perform in this regard, while others consistently ran the indirect pursuit as indicated. Since the results for both right- and left-handed problems are comparable, these have been counted together under the following general categories:

A: Both γ_p and θ_p are *distinctly* compensated. This corresponds to a distinct turn both down and to the right, as shown in Figures 110 and 111.

B: Only γ_p is distinctly compensated. As shown in Figures 110 and 111, the spider turns distinctly down, but turns either to the left or to an intermediate position in the horizontal plane projection.

C: Only θ_p is distinctly compensated. As shown in Figures 110 and 111, the spider makes a distinct turn to the right, but turns either up or in an intermediate direction in the vertical plane projection.

D: Neither γ_p nor θ_p is distinctly compensated for movement.

The table includes a small number of trials (in parentheses) in which the spider ran down, rather than up, to a secondary objective. In this case the categories given above are equally applicable, but a compensated γ_p is up, rather than down.

SN	N	A	B	C	D
3fPUL	5	4	1	0	0
5fPUL	1	1	0	0	0
9fPUL	6	4(1)	2	0	0
11fPUL	52	40(1)	2	9	1
13fPUL	59	49	7	3	0
16mPUL	12	10	2	0	0
17mPUL	37	31	4	1	1
18mPUL	30	23(2)	2	5	0
total PUL	202	162(4)	20	18	2

Compensation of both γ_p (A + B) and θ_p (A + C) occurs in a highly significant ($P < 0.0001$) majority of the trials. Note that these data are consistent with the generalization that these spiders compensate in each dimension 90% of the time, and that the probability of compensation in one dimension is independent of the probability of compensation in the other dimension. In a significant number of trials (38/202), compensation occurs in one dimension in the absence of distinct compensation in the other dimension.

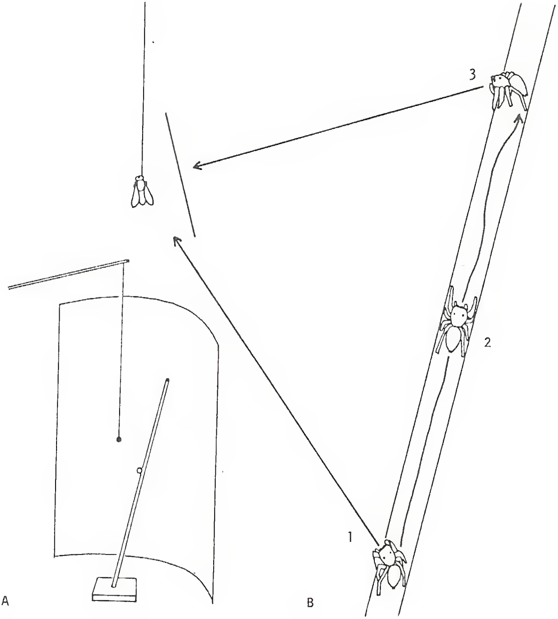


Figure 114. Simple demonstration of compensation for movement on a skewed route (inclined) in space. A: The spider (open circle) runs on a wood dowel inclined 45-60° with reference to the horizontal. Prey is presented against a partial cylindrical screen of heavy white paper as shown. B: Detail of a pursuit on a skewed route. After orientation to the lure (1), the spider runs along the route as the lure is removed (2). The change in both θ (significantly larger) and γ (turn down rather than up) components of the reorientation (3) can be readily discerned by an observer. In this situation, the reference systems available to the spider during the pursuit are, presumably, the θ and γ systems. Even against a uniform white wall, as shown here, no additional reference systems are required to determine an appropriate direction of reorientation (see Figure 115).

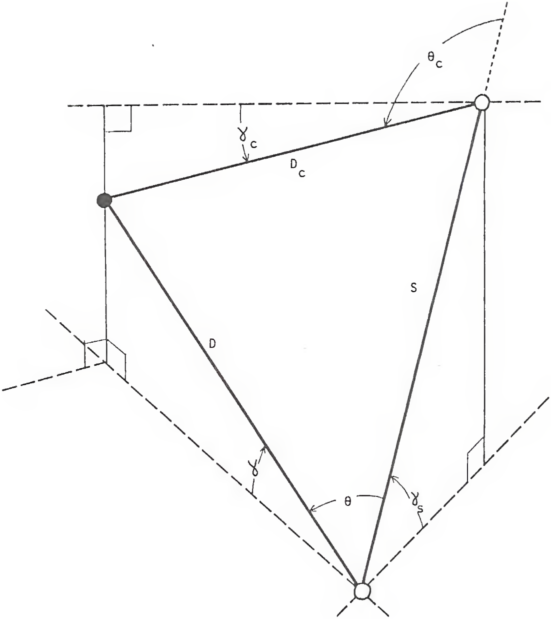


Figure 115. Analysis of requisite information for movement compensation during the segment of indirect pursuit shown in Figure 114: Determination of γ_c and θ_c for reorientation. In this diagram, each of the dashed lines is horizontal. Both the initial spider-to-prey vector (magnitude D) and the route vector (magnitude S) are skewed in space. this analysis is based upon the use of a γ-θ reference system by the spider. The direction of reorientation with reference to gravity (γ_c) is a function of D, S, θ, γ, and γ_s. In comparison the reorientation angle with reference to the direction of movement (θ_c) is a function of only three variables: D, S, and θ. Since the information corresponding to the determination of a specific value of θ_c constitutes a subset (three variables) of the requisite information for the determination of γ_c (five variables), the ability to compensate for movement in the θ reference system may be considered implicit in the ability to compensate for movement in the γ reference system.

orientation presents no problem for the determination of movement compensation: No compensation is required in this system as the radial direction of the prey remains constant with reference to the direction of the route. Thus movement compensation is basically relevant to the θ and γ reference systems.

In theory, compensation for movement in space in the determination of θ_r and γ_r (as approximations of θ_c and γ_c, respectively) is simple: The vector of movement during pursuit (magnitude S) must be subtracted from the initial spider-to-prey vector (magnitude D), to determine the new spider-to-prey vector (magnitude D_c):

$$\vec{D}_c = \vec{D} - \vec{S}$$

Figure 115 provides an analysis of the information content of this problem, with respect to the use of spider-centered θ and γ reference systems to determine prey direction. Based upon the relationships shown in Figure 115:

$$\theta_c = \sin^{-1}\left[\frac{D \sin \theta}{(D^2 - 2DS \cos \theta + S^2)^{\frac{1}{2}}}\right]$$

And:

$$\gamma_c = \sin^{-1}\left[\frac{D \sin \gamma - S \sin \gamma_s}{(D^2 - 2DS \cos \theta + S^2)^{\frac{1}{2}}}\right]$$

A most interesting conclusion emerges from this analysis: An ability to integrate information (D, θ, and S) which is determinative of θ_c, is required for the determination of γ_c; the latter is a function of γ and γ_s (as defined in Figure 115), in addition to D, θ, and S. If *Phidippus* can determine γ_c with some accuracy, then it must also have the information necessary for the determination of θ_c with similar accuracy; θ orientation plays an imperative role in movement compensation within the fixed γ reference system. By similar analysis, an appraisal of the new prey distance (D_c) is also implicit in the ability to determine γ_c:

$$D_c = (D^2 - 2DS \cos \theta + S^2)^{\frac{1}{2}}$$

Again this analysis leads to a most interesting conclusion, since D_c, in concert with γ_c and θ_c, completes the definition of the new prey position: If Phidippus can determine an accurate approximation of γ_c, then it must also have all of the information required to determine the actual position of that prey with similar accuracy. This is equivalent to stating that the spider always knows (again, with a certain accuracy) the relative position of prey during a pursuit, or at least has the ability to make this determination. This can explain why Phidippus execute such smooth and directed reorientation turns during pursuit. All of this assumes continuous and total integration of all the information which can be gathered by the spider.

As shown in Figure 111, a Phidippus can transpose its knowledge of prey position between the θ and radial (visual) orientation systems. Since the θ system is required for the effective use of the γ system as well, one can conclude that these systems (each representing a form of information available to the spider) are not employed independently during the pursuit. Each system contributes to what is at least the functional equivalent of what we, based upon our own subjective experience of that which we term reality, might describe as an integrated world view based upon the fixity of three-dimensional space (space constancy, irrespective of our own movement in that space).

The foregoing analysis is consistent with more than the constraint imposed by solid geometry: It also agrees with all of the observations and measurements of the indirect pursuit which have been collected in the course of this study. A large part of the evidence for this general theory comes from the demonstrated ability of Phidippus to utilize estimates of D, θ, and S to determine θ_c. This, of course, is a major prediction of the general theory. The ability of these spiders to use an integrated appraisal of both γ and D (as in preparation for a jump) is also consistent with this interpretation, as is their ability to gather and retain γ information in general. The latter ability applies to both the direction of prey with reference to gravity (γ), and the inclination of the route of pursuit (γ_s). Thus the total result (an ability to maintain a memory of prey position during indirect pursuit) can be explained by the ability of Phidippus to integrate precisely those forms of information which have been demonstrated to exist: D, γ, θ, γ_s, S, and visual cues specifying radial direction, if necessary. In this appreciable task one can safely assume that salticids are no more familiar with our mathematical systems than are our own nervous systems when engaged in the performance of similar feats: In both cases, analog computations, hidden somewhere deep within the central nervous system, should suffice.

SECTION XIV
CONCLUDING DISCUSSION

Orientation (alignment with a particular direction in space) exists only within the context of a sequence of behavior which requires this sense of direction. For this study a segment of the indirect pursuit of prey by the salticid Phidippus, and more specifically the reorientation turn (toward the expected position of the prey) which comes at the end of each segment of pursuit, has been of critical importance in this regard. As far as can be determined, the execution of a distinct reorientation turn to prey during an indirect pursuit of that prey is uniquely a feature of salticid behavior, among the chelicerates. This "facing" behavior is clearly related to the extraordinary development, and use, of vision by spiders of this family.

One might ask, then, how the behavior of a jumping spider can be related to the behavior of other spiders. Apart from the extreme development of the eyes and visual centers, the basic organization of the nervous system of the salticid does not differ greatly from that of other spiders (Hill, 1975). The cuticular sense organs of salticids also compare with those of other spiders (Hill, 1977a). Even the ability to scan objects with the anterior medial eyes (AME) is not restricted to the Salticidae; both thomisids and lycosids also move the retinae of the AME, although the AME and associated musculature of these spiders are comparatively simple (Homann, 1971). Despite the uncertain phylogenetic relationship of families within the order

Araneae, representatives of different families can be expected to utilize common mechanisms in their respective orientations.

As noted above, orientation is observed in the context of a particular sequence of behavior. To date, the study of spider orientation has been restricted to relatively few sequences of behavior. As an example, the ability of Agelena (Agelenidae) to locate its retreat after a foray upon the funnel web has been used to demonstrate the ability of these spiders to remember the direction of the retreat with reference to either gravity (Holzapfel, 1933), visual cues (Görner, 1958), or the immediate direction of movement (Moller, 1970). These reference directions correspond to those which can be employed by Phidippus during its pursuit of prey, although they emerge from a different context of behavior. Further study of the oriented movement of other two-clawed hunting spiders which dwell upon plants (such as the Clubionidae and the Thomisidae) is highly desirable for purposes of comparison with the orientation of salticids.

It is significant that the same information which is remembered and integrated into the execution of a reorientation turn by Phidippus is also utilized in other sequences of behavior. As a specific example, γ information is an immediate determinant of jumping behavior; it can also be utilized in a subsequent reorientation.

The time scale of short-term memory of the relative prey position is also of great interest. Presumably γ, D, and any visual associations (including radial orientation) with the direction of prey can be remembered as the spider faces the prey position directly, to establish a primary objective. The direction of the route of access with regard to this prey direction (θ information) does play a role in route selection, prior to a turn away from the prey to initiate the pursuit; the actual magnitude of θ may be determined by the spider during the execution of this turn, however. The latter interpretation agrees with the close relationship between directional information and the turning angle of salticids, as demonstrated by the study of their initial orientation turns to face certain visual stimuli (Land, 1971). Evaluation of the inclination (γ_s) and magnitude (S) of the pursuit vector presumably accompanies that movement. Add to this the ability to transpose between θ and radial (visual) reference systems during a single segment of pursuit, and the necessity for an internal relatedness of different reference systems working in concert becomes obvious: Data collected by means of wholly different sensory modalities, at different points in time, are integrated into an appropriate output, the reorientation turn.

Like the orientation turn to face a visual stimulus, which _can_ be executed accurately in the absence of visual feedback (Land, 1971), the reorientation turn is based upon an internal directive. Given any one of the three basic reference systems considered here (θ, γ, and radial), feedback is always available from the corresponding sensory modality to put a brake upon the respective component of the reorientation turn. As probably applies to the orientation turn as well, feedback can presumably be used for this purpose when it is available. Yet the two directional components of the reorientation are generally combined in the execution of a single, and direct, turn. Certainly the animal does not search until an appropriate direction is found for each component. These are _directed turns_, and much information with regard to the orientation of the prosoma in each reference system is assuredly gathered prior to the execution of the reorientation turn.

In retrospect, it almost appears that one could deduce many of the results of this experimental study from the simple fact that Phidippus must capture prey which are separated in space by indirect routes of access. To do so, they must be able to complete a detour. To complete a detour, the spider must be able to locate the detour with its vision; it must also remember the location of the objective of its pursuit. For this memory, only a limited number of reference directions are available to the spider, based upon the corresponding sensory modalities, and these must be employed within the constraints imposed by geometry. Orientation with reference to the direction of movement (θ orientation) is virtually implicit in the ability to compensate for movement (space constancy) in the context of any other reference system, apart from the visual information which specifies a direction in a plane perpendicular to the direction of movement.

Like all stories in the real world, this one has not come to an end. The same features of orientation which apply to the pursuit of sighted prey by a salticid most certainly apply to the directed movement of these spiders upon plants in general, but what are the underlying directives of this movement? This question relates to the question of habitat selection by Phidippus; different species within this genus tend to situate themselves in different places, or microhabitats (Gertsch and Riechert, 1976), but the behavioral correlates of this habitat partitioning have not been explored.

Considering the remarkable development of the anterior medial eyes (AME) of the salticid spider (Land, 1969a, 1969b; Eakin and Brandenburger, 1971), the ability of these spiders to recognize specific, and perhaps complex, forms is of particular interest. The ability to recognize the elements of plant structure, and particular features of plant configuration, is certainly relevant to the orientation of _Phidippus_ during its pursuit of prey. Perhaps these spiders can also recall specific features, or landmarks, within their hunting range. There is a good possibility that _Phidippus_ can recognize specific plant configurations associated with the site of the resting sac. One can always ask: What does the spider see? And: What does it know? The answers to these questions must be taken, indirectly, in terms of what the spider _does_.

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BIOGRAPHICAL SKETCH

David Edwin Hill was born on December 31, 1948, in Elmhurst, Illinois. His childhood was passed in the communities of Groveland and Deephaven, near Lake Minnetonka in Minnesota; perhaps the most influential book, with respect to his early experience in Biology, was a copy of Insect Stamps kindly given to young David by his mother. After the passage of a considerable amount of time, David completed his local schooling and entered the University of Minnesota in November of 1966. Drafted into the U. S. Army, he completed his service as a medical laboratory technician in San Francisco and Nha Trang, Republic of Viet Nam, emerging from this experience as an unemployed Specialist V. Returning to the University of Minnesota with new determination (and funding, provided by the G. I. Bill) in the autumn of 1971, David completed his B. S. in the College of Biological Sciences in June of 1973. By this time he had married Rose Marie, who, incidentally, had grown up in New York City prior to settling in Utah. David went on to complete his M. S. at Oregon State University in 1975, then moved his growing family to the University of Iowa for a year. In September of 1976, David transferred to the University of Florida to complete his graduate work.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Jonathan Reiskind, Chairman
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John F. Anderson
John F. Anderson
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

James E. Lloyd
Professor of Entomology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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